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REVIEW

Hydrogen sulfide (H_2S) signaling in plant development and stress responses

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Abstract Hydrogen sulfide (H_2S) was initially recognized as a toxic gas and its biological functions in mammalian cells have been gradually discovered during the past decades. In the latest decade, numerous studies have revealed that H_2S has versatile functions in plants as well. In this review, we summarize H_2S-mediated sulfur metabolic pathways, as well as the progress in the recognition of its biological functions in plant growth and development, particularly its physiological functions in biotic and abiotic stress responses. Besides direct chemical reactions, nitric oxide (NO) and hydrogen peroxide (H_2O_2) have complex relationships with H_2S in plant signaling, both of which mediate protein post-translational modification (PTM) to attack the cysteine residues. We also discuss recent progress in the research on the three types of PTMs and their biological functions in plants. Finally, we propose the relevant issues that need to be addressed in the future research.

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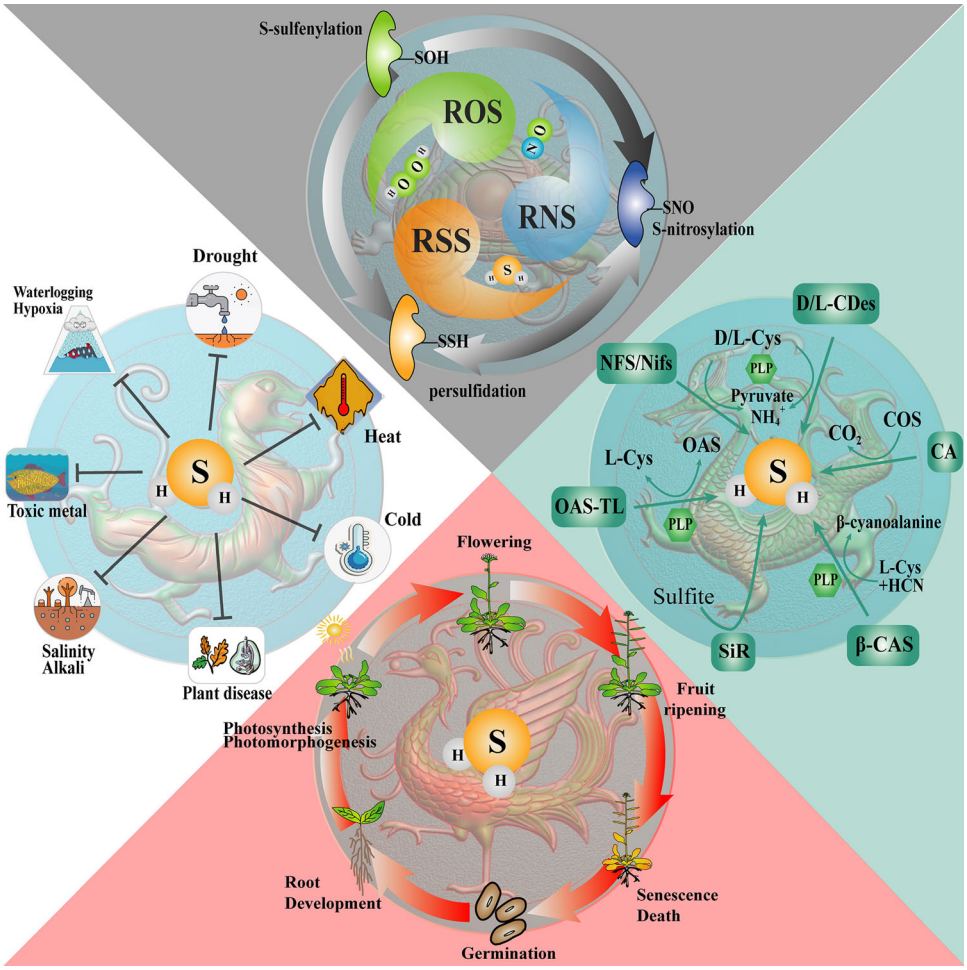
Graphic abstract



Keywords Hydrogen sulfide, Nitric oxide, Reactive oxygen species, Sulfur metabolism, Biotic and abiotic stresses, Growth and development, Persulfidation, S-Sulfenylation, S-Nitrosylation

INTRODUCTION

For hundreds of years since its discovery, hydrogen sulfide (H_2S) has been regarded as a gas with an unpleasant odor and high toxicity (Fu et al. 2018b; Lefer 2019). In the early research, much attention was paid to the risk of excessive H_2S exposure for animals, plants and microorganisms. Until recent decades, H_2S was gradually found to act as a signal molecule involved in the regulation of biological and physiological processes. Particularly, with increasing knowledge about the role of nitric oxide (NO) and carbon monoxide (CO) as signaling molecules in mammalian and plant physiology research (Burnett et al. 1992; Snyder 1992; Wu and Wang 2005), the unique identity of H_2S as a new gasotransmitter has been gradually revealed (Wang 2002) (Fig. S1). In mammals, endogenous H_2S controls a variety of physiological processes and participates in the regulation of the pathogenesis of various diseases, including hypertension, atherosclerosis, angiogenesis and myocardial infarcts (Wang 2012; Wen et al. 2018). There has been increasing evidence showing the signaling role of H_2S in plants. Different from the role as a phytotoxin at high concentrations, H_2S at low concentrations has been shown to play critical roles in diverse processes of plant life cycle, such as plant growth, development, and biotic and abiotic stress responses (Chen et al. 2011; Fu et al. 2018b; Jin et al. 2013; Luo et al. 2020) (Fig. S2).

ENDOGENOUS PRODUCTION OF H_2S IN PLANTS

Understanding the production of endogenous H_2S is a critical prerequisite for clarifying the role of H_2S in various biological and physiological processes. To analyze the enzymes related to the production of H_2S in plants, it is necessary to review the corresponding enzymes in animals first. In mammals, H_2S biogenesis is catalyzed by the enzymes in the trans-sulfuration pathway, namely cystathionine β-synthase (CBS) and cystathionine γ-lyase (CSE), and occurs in the cytoplasm (Kabil and Banerjee 2014). CBS catalyzes the β-substitution of serine with homocysteine to form cystathionine and H_2O, which is kinetically the most efficient H_2S-producing reaction. When cysteine replaces serine as the substrate, the reaction products will be cysteine and H_2S. In addition, CBS also catalyzes cysteine to generate H_2S through extra β-substitution reactions (Chiku et al. 2009; Kabil and Banerjee 2014; Kabil et al. 2011; Singh et al. 2009). CSE, a homotetrameric enzyme, can decompose cystathionine to form cysteine, ammonia and α-ketobutyrate. Due to the inclusiveness of its substrate-binding domain, CSE can directly combine and catalyze homocysteine and cysteine to produce H_2S (Kabil and Banerjee 2014; Singh et al. 2009). Another enzyme, 3-mercaptopyruvate sulfurtransferase (3-MST), also contributes to the production of endogenous H_2S from 3-mercaptopyruvate. Aspartate aminotransferase (AAT)/cysteine aminotransferase catalyzes the transamination reaction between cysteine and α-ketoglutarate (Kimura et al. 2013). Subsequently, 3-MST transfers the sulfur to a nucleophilic cysteine in the active site to yield persulfide and pyruvate (Shibuya et al. 2009). Among the three aforementioned H_2S-producing enzymes which have been validated in mammals, CBS and 3-MST have homologs in plants, indicating that they may play potential roles in the production of H_2S in plants. However, there is still a lack of solid evidence for the existence of CSE homologous genes in plants.

D/L-Cysteine desulfhydrase (D/L-CDes)

The exploration of H_2S-producing enzymes in plants can be traced back to the mid-1960s. Tishel and Mazelis (1966) identified the activity of D/L-cysteine lyase in cabbage leaves, and H_2S together with pyruvate and ammonia was found in the homogenate. It was not until 1980 that Harrington and Smith validated the existence of L-cysteine desulfhydrase [L-CDes; EC 4.4.1.28] in tobacco cells by the S^{35}-labeled L-cysteine isotope method (Harrington and Smith 1980). After decades of exploration, D-cysteine desulfhydrase [D-CDes; EC 4.4.1.15] was successfully identified in *Arabidopsis* (*Arabidopsis thaliana*) (Papenbrock et al. 2007; Riemenschneider et al. 2005). In *Arabidopsis,* four cysteine desulfhydrase (CDes) genes have been reported, including L-cysteine desulfhydrase (LCD, At3g62130), L-cysteine desulfhydrase 1 (DES1, At5g28030) (Álvarez et al. 2010), D-cysteine desulfhydrase 1 (DCD1, At1g48420) and D-cysteine desulfhydrase 2 (DCD2, At3g26115) (Hou et al. 2016; Riemenschneider et al. 2005). The common characteristic of these genes is that they all require the participation of coenzyme 5′-pyridoxal phosphate (PLP) for the degradation of cysteine to produce H_2S, ammonia and pyruvate in a stoichiometric ratio of 1:1:1 (Papenbrock et al. 2007). The only difference lies in the chirality of the substrates: the substrate of LCD and DES1 is L-cysteine, while that of DCD1 is D-cysteine. The most special one is DCD2, which can degrade the two isomers of cysteine (Riemenschneider et al. 2005). The production of endogenous H_2S via CDes has been confirmed in various physiological and developmental processes of plants (Kaya and Ashraf 2020; Shen et al. 2013), especially DES1 and LCD, which use L-cysteine as the substrate, are the most widespread in plants. The important functions of these two genes will be discussed in detail later. With the progress in research, more CDes homologues have been cloned in different species, such as *OsDCD1* and *OsLCD2* in rice (Shen et al. 2019; Zhou et al. 2020), and *BnDES1* in *Brassica* (*Brassica napus*) (Xie et al. 2013).

In addition, nitrogenase Fe–S cluster (NFS/Nifs) is also a putative H_2S-producing enzyme with L-cysteine desulfhydrase-like activity (Pilon-Smits et al. 2002). AtNFS1 (At5g65720) and AtNFS2 (At1g08490) play an important role in the formation of Fe–S clusters, and can produce L-alanine and elemental S with the participation of PLP in *Arabidopsis* (Leon et al. 2002). H_2S can be produced with the availability of an appropriate amount of reducing agent to provide electrons (Jez and Dey 2013; Leon et al. 2002; Pilon-Smits et al. 2002).

O-Acetylserine(thiol)lyase (OAS-TL)

Another enzyme is *O*-acetylserine(thiol)lyase [OAS-TL; EC 2.5.1.47], which plays a major role in the last step of cysteine synthesis (Tai and Cook 2000). In the process of cysteine synthesis, serine acetyltransferase (SAT) catalyzes acetyl-CoA and serine to form *O*-acetylserine (OAS); then, OAS-TL catalyzes OAS and sulfide (i.e., H_2S) to synthesize cysteine (Álvarez et al. 2010; Heeg et al. 2008; Ravina et al. 2002). The latter step also requires the participation of coenzyme PLP. In *Arabidopsis*, nine OAS-TL family genes have been identified, including DES1 mentioned above. The main catalysts for cysteine

synthesis include OASA1 (At4g41880), OASB (At2g43750) and OASC (At3g03630), which are subcellularly localized in the cytoplasm, chloroplast and mitochondria (Álvarez et al. 2010; Wirtz and Hell 2006), respectively. Other family members have different or unidentified functions. In fact, there is a lack of in vivo experimental evidence for the ability of OAS-TL to generate H_2S. Since OAS-TL could generate H_2S in some in vitro experiments, some studies have concluded that the enzymatic reaction of OAS-TL is a reversible process that can generate endogenous H_2S. In this regard, we speculate that OAS-TL has bidirectional catalytic activity, but its ability to produce endogenous H_2S in the plants is almost completely suppressed. This also explains the emergence of DES1 in addition to OAS-TL in *Arabidopsis* from an evolutionary point of view, and why *des1* and *oasa1* mutations resulted in opposite phenotypes under toxic metal stress.

β-Cyanoalanine synthase (*β*-CAS)

Cyanide (CN^-), another cytotoxic molecule found after NO, CO and H_2S, inhibits the electron transport activity in the chloroplasts and mitochondria via binding to cytochrome oxidase (COX) or other metalloenzymes (Yamasaki et al. 2001). Even so, cyanide is still produced in plants and germs. In higher plants, to detoxify the cyanide emerging within the cells, *β*-cyanoalanine synthase [*β*-CAS; EC 4.4.1.9] catalyzes the reaction between L-cysteine and HCN to synthesize *β*-cyanoalanine and H_2S (Yamasaki et al. 2019), which also requires the participation of PLP. As mentioned above, 3-MST in mammals also catalyzes a similar reaction with 3-mercaptopyruvate as the sulfur donor. In *Arabidopsis*, *β-CAS* genes, including *CYSC1*, *CYSD1* and *CYSD2*, are also members of the *OAS-TL* gene family, but with different active domains (Yamaguchi et al. 2000). The mitochondrial *CYSC1* is involved in root hair formation (García et al. 2010) at the early stage of this pathway (Arenas-Alfonseca et al. 2018a, b). Besides, *CYSC1* is also considered to be responsive to water deficiency and pathogen infection in *Arabidopsis* (García et al. 2013; Machingura et al. 2013), which is consistent with the H_2S response model introduced later.

Carbonic anhydrase (CA)

Unlike that of the three enzymes mentioned above, the relationship of carbonic anhydrase [CA; EC 4.2.1.1] with H_2S seems not to have been fully revealed. However, there have been some earlier reports about the catalysis of CA on carbonyl sulfide (COS), the most abundant sulfur gas in the atmosphere (Watts 2000), to produce carbon dioxide (CO_2) and H_2S via hydrolytic reaction (Notni et al. 2007). Many green plants can absorb COS in the air through the stomata, and then assimilate and store the required sulfide through CA catalytic reactions (Bloem et al. 2012). When the absorption of sulfate in plant roots is blocked, the above reaction would occur as a compensation (Bloem et al. 2011; Yamasaki and Cohen 2016). Interestingly, COS increases stomatal conductance, but the response was disrupted in CA-deficient antisense lines (Stimler et al. 2012). Through a test of the stomatal responses against COS in 22 plant species, Stimler et al. (2012) proposed that CA is a plausible H_2S-producing enzyme in plants. However, there is still a lack of more intuitive evidence on the mechanism of COS uptake and endogenous H_2S production in plants.

H_2S PLAYS A ROLE IN PLANT SULFUR METABOLISM

As a signal molecule in organisms, H_2S is involved in various physiological activities with different signal pathways. Moreover, it is an endogenous sulfide and a key node of sulfur metabolism in organisms. Besides, sulfur is essential for all living organisms on Earth as a key component of amino acids (i.e., cysteine and methionine), polypeptide glutathione (GSH), several group transfer coenzymes and vitamins (Romero et al. 2014). Mammals ingest S-amino acid methionine through the diet, while inorganic sulfur is reduced to cysteine through the assimilation pathway of reducing sulfate in plants.

For plants, there are two routes for the absorption of S elements, namely root uptake and gas exchange through stomata (Notni et al. 2007), with the former as the main route (Fig. 1). In agriculture, sulfur is widely applied in the form of sulfate fertilizers (Fuentes-Lara et al. 2019), and transported by a proton/sulfate co-transport mode mediated by sulfate transporters (SULTRs) in root epidermal cells (Buchner et al. 2004). Subsequently, the sulfate is loaded into the xylem vessels and distributed into the entire plant (Leustek et al. 2000), which is stored into vacuoles via SULTR4:1 (Takahashi et al. 2011) or transported to chloroplasts via SULTR3:1 to launch the assimilatory activities (Gotor et al. 2015). After entry into the chloroplasts, sulfate is activated to adenosine 5′-phosphosulfate (APS) under the catalysis by ATP sulfurylase. As an intermediate, APS is further reduced to sulfite via the APS reductase (APR) with GSH as the reducing molecule (Birke et al. 2015). Subsequently, through a six-electron reaction with reduced ferredoxin as a reductant, sulfite is reduced to sulfide under the catalysis by sulfite reductase (SiR) (Fu

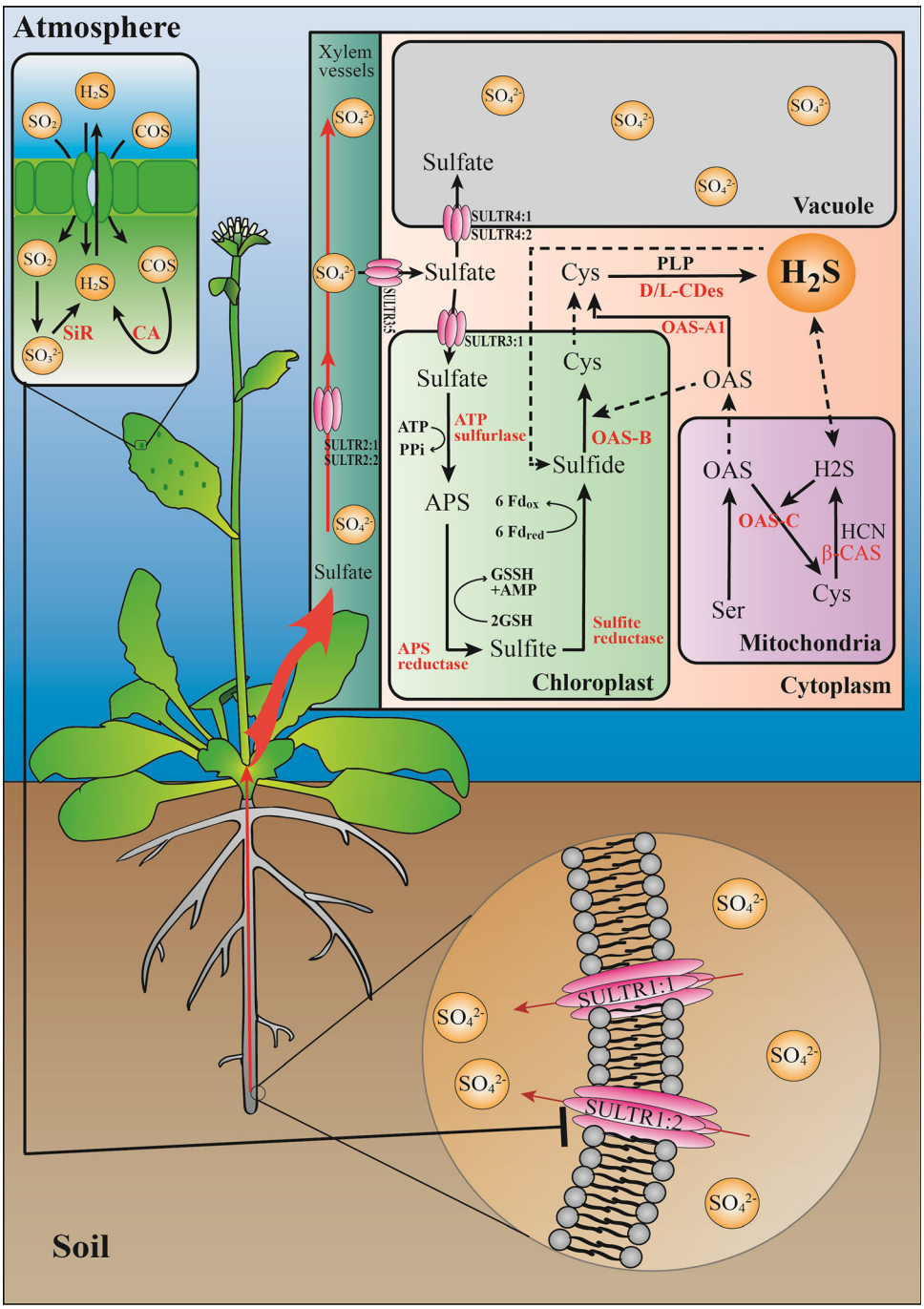


Fig. 1 H_2S acts as a node in plant sulfur metabolism. The transport of sulfate from roots is the main way for plants to absorb S elements, which are then transported to all parts of the plant through the xylem vessels. Part of the sulfate entering the cells will be stored in vacuoles, and the other part will enter the assimilation pathway in the chloroplast. After being activated to APS, sulfate is further reduced to sulfite via APS reductase with GSH as the reducing molecule. Then, through a six-electron reaction with reduced ferredoxin, sulfite is reduced to sulfide under the catalysis by SiR. The produced sulfide is a substrate for the synthesis of cysteine. Together with OAS, cysteine is synthesized under the catalysis of OAS-TL enzyme. Cysteine can be degraded to generate H_2S by CDes. Another mode for obtaining S elements is from the atmosphere. H_2S, COS and SO_2 are captured by plants through the stomata. COS can be hydrolyzed to produce H_2S under the action of CA, while SO_2 can be hydrolyzed into sulfite and enter the assimilation pathway. The two absorption pathways interact and restrain each other

et al. 2018b). These sulfides are S donors required for the synthesis of cysteine. Since H_2S belongs to sulfides, SiR is considered as a major enzyme of H_2S production in plastids (Filipovic et al. 2018). Besides sulfur assimilation, cysteine can be degraded to generate H_2S. The second route for plants to obtain S is from the atmosphere, and COS is one of the S-containing gases captured by plants through the stomata (Fig. 1). In addition, many other sulfur-containing gases, such as H_2S, SO_2 and SO_3, also sneak into plants in this way. Among them, COS and SO_2 can promote the generation of endogenous H_2S in plants through different metabolic pathways (Baillie et al. 2016; Notni et al. 2007). It is worth noting that SO_2 can also induce stomatal closure like H_2S, but in a much less efficient way (Baillie et al. 2016).

The synthesis of cysteine is closely associated with the function of OAS-TL. In *Arabidopsis*, OASA1 plays a major catalytic role; OASB and OASC play a redundant role; and OASC mainly maintains the dynamic balance of

OAS in mitochondria, which actively catalyzes cysteine synthesis only in the deficiency of both OASA1 and OASB (Heeg et al. 2008). DES1 appears to belong to L-CDes and catalyzes the decomposition of L-cysteine to H_2S. Exogenous application of H_2S to *Arabidopsis* would enhance the activity of OAS-TL and the production of cysteine (Khan et al. 2018). The exogenous cysteine also directly promotes the production of endogenous H_2S, not only through the decomposition of L-CDes, but also through the increased synthesis of abscisic acid (ABA), resulting in enhanced expression and activity of DES1 (Batool et al. 2018). Under some abiotic stress conditions such as cadmium (Cd) stress, the *oasa1* mutant showed significant sensitivity (Lopez-Martin et al. 2008). On the contrary, the *des1* mutant showed significantly enhanced tolerance to Cd (Álvarez et al. 2010). This may be related to the different effects of OASA1 and DES1 on intracellular cysteine homeostasis. Evidently, the total intracellular cysteine content was reduced by approximately 35% in the *oasa1* mutant and increased by approximately 25% in the *des1* mutant relative to the wild type (WT) (Lopez-Martin et al. 2008; Romero et al. 2014). Considering that OAS-TL in *Arabidopsis* root cells can interact with SULTR2;1 and inhibit its sulfate transporting activity (Shibagaki and Grossman 2010), the inhibition of SULTR expression by the supply of cysteine to plant roots or fumigation with H_2S and SO_2 could be ascribed to the enhancement of OAS-TL enzyme activity by endogenous H_2S (Herschbach et al. 1995; Vauclare et al. 2002). In areas with high levels of atmospheric H_2S, the capacity of root sulfate transporters of wild plants and crops is usually weakened, and vice versa.

H_2S POSITIVELY RESPONDS TO BIOTIC AND ABIOTIC STRESSES IN PLANTS

As a small gaseous signaling molecule, H_2S readily traverses the intracellular and intercellular domains, and plays a key role in regulating the homeostasis in plant cells (Papanatsiou et al. 2015). H_2S has been identified as a brilliant defender against different stresses such as drought, heat, chilling, heavy metals, osmotic and saline (Pandey and Gautam 2020) (Fig. 2). In addition, a growing body of research has revealed the crosstalk between H_2S and various signaling pathways, indicating its key role in the protection of plants against stresses (Banerjee et al. 2018). With increasing knowledge about the action and regulation associated with H_2S, it becomes possible to generalize the protective role of H_2S in plant stress responses.

Classic model for the alleviation of abiotic stress by H_2S in plants

H_2S can help the plants to resist a variety of abiotic stresses such as drought, cold, heat, salinity, hypoxia and toxic metal to effectively alleviate their damages (Pandey and Gautam 2020; Zhang et al. 2021), which is closely associated with the classic "rescue" mode of H_2S. Continuous exposure to any abiotic stress will cause an imbalance of endogenous redox homeostasis. Excessive accumulations of reactive oxygen species (ROS), hydrogen peroxide (H_2O_2) and superoxide anion ($O_2^{-\bullet}$), will further lead to lipid peroxidation, protein oxidation and damage to plant cells, resulting in autophagy and programmed cell death (PCD) (Da-Silva and Modolo 2018; Hancock 2017). Many studies have demonstrated that exogenous H_2S treatment can alleviate oxidative stress by increasing the expression and activities of some enzymes, such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), polyphenol oxidase (PPO), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and guaiacol peroxidase (GPX) (Aghdam et al. 2018; Christou et al. 2014; Fu et al. 2013; Guo et al. 2018; Khan et al. 2018; Li et al. 2015b, 2019; Luo et al. 2015; Ma et al. 2016; Shan et al. 2018; Shen et al. 2013; Wei et al. 2019; Yang et al. 2016; Ye et al. 2020) (Fig. 2). Recently, H_2S was found to enhance the activity of antioxidant enzymes in plants (Amooaghaie et al. 2017; Dawood et al. 2012; Kaya et al. 2018; Li et al. 2012a, 2020b; Sun et al. 2013; Zhang et al. 2015b), which is considered to be related to H_2S-mediated post-translational modification (PTM). We will discuss this in detail later.

Moreover, H_2S can maintain the redox balance and prevent further apoptosis by dynamic regulation of the NADPH oxidase and antioxidant enzyme systems (Kolupaev et al. 2017; Yang et al. 2016). H_2S facilitates the production of more H_2O_2 by NADPH oxidase through the enhancement of transcription and enzyme activity, and controls antioxidant enzymes to reduce ROS content in a similar way (Christou et al. 2014; Li et al. 2015b; Yang et al. 2016; Ye et al. 2020). Such functional difference seems to be related to the ratio between the ROS and H_2S levels. When the accumulation of ROS causes oxidative stress, the increased H_2S will reduce the ROS level through enzymatic and non-enzymatic pathways. However, when H_2S acts as a driving signal to regulate stomatal movement, RBOHs will be induced to increase endogenous ROS, thus, initiating the downstream signal. Studies of mammals have shown that H_2S increases GSH by enhancing the activity of γ-glutamylcysteine (γ-CE) synthetase and cystine

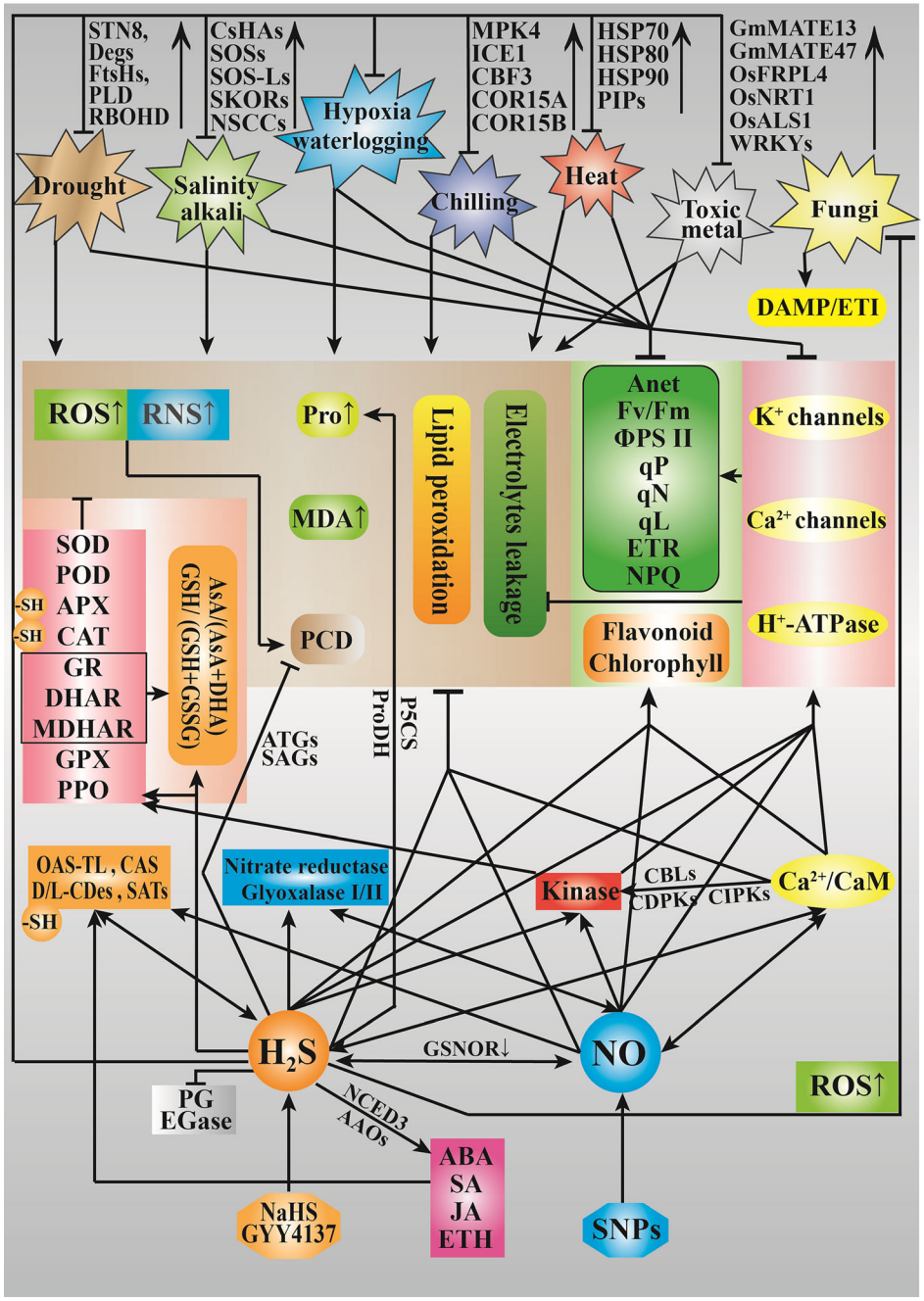


Fig. 2 H_2S positively responds to biotic and abiotic stresses in plants. The brown shadow is the items related to oxidative damage; yellow shadow is the antioxidant system; green shadow is the photosynthetic system and pigments; and pink shadow is transporters. AAOs, ABA-aldehyde oxidase; ALS, aluminum sensitive; APX, ascorbate peroxidase; ATGs, autophagy proteins; CAS, cyanoalanine synthase; CaM, calmodulin; CAT, catalase; CBF, C-repeat-binding factors; CBL, calcineurin B-like proteins; CDPK, Ca-dependent protein kinase; CIPK, CBL-interacting protein; COR15, cold responsive 15; Deg, D1 protein degradation-related genes; DHAR, dehydroascorbate reductase; D/L-CDes, D/L-cysteine desulfhydrase; EL, electrolyte leakage; EGase, endo-β-1,4-glucanase; ETR, electron transfer rate; Fv/Fm, potential photochemical efficiency; GSNOR, S-nitrosoglutathione reductase; GR, glutathione reductase; HA, proton pump; Hsp, heat shock protein; H_2S, hydrogen sulfide; ICE, inducer of CBF expression; MDA, malondialdehyde; MDHAR, monodehydroascorbate reductase; NCED, 9-cis-epoxy-carotenoid dioxygenase; NO, nitric oxide; NPQ, non-photochemical quenching; NRT, nitrate transporter; OAS-TL, *O*-acetylserine (thiol)lyase; PCD, programmed cell death; PDH: proline dehydrogenase; PG, polygalacturonase; PLD, phospholipase D isoforms; PIPs, aquaporins; POD, peroxidase; PPO, polyphenol oxidase; Pro, proline; P5CS, proline synthase; qN, non-photochemical quenching; qP, photochemical quenching; ROS, reactive oxygen species; RNS, reactive nitrogen species; SATs, serine acetyltransferase; SAGs, senescence-associated genes; SOD: superoxide dismutase; SOS, salt overly sensitive; STN8, D1 protein phosphatase; ΦPS II, actual photochemical efficiency; –SH, persulfidation. Arrowheads indicate positive regulatory interaction and flat arrow heads indicate negative regulation

transport (Kimura and Kimura 2004). A latest study of plants also demonstrated that H_2S increases GSH, the reduced/oxidized GSH (GSH/GSSG) ratio, and the expression of GSH-associated genes (*GST Tau*, *MAAI*, *APX*, *GR*, *GS* and *MDHAR*) under chilling stress (Liu et al. 2020c). In addition, both H_2S and H_2O_2 were also discovered to participate in the up-regulation of ascorbic acid (AsA)-GSH cycle in plant tissues, which acts as the downstream signal for the regulation of H_2S on ROS (Mostofa et al. 2015; Shan et al. 2018). Besides, the increases in malondialdehyde (MDA), electrolyte leakage (EL) and proline (Pro) caused by abiotic stress are also important indicators to reflect the oxidative damage of plants. Exogenous spraying or fumigating with H_2S on plant seedlings could also significantly inhibit the increase in the activity of MDA, EL and Pro (Da-Silva and Modolo 2018; Kaya and Ashraf 2020; Shan et al. 2018).

The activation of H_2S-related enzymes is also a main way for exogenous H_2S to alleviate the effect of different stresses. Exogenous application of NaHS can not only increase the activities of D/L-CDes, OAS-TL, CAS and CA enzymes, but also elevate the content of endogenous cysteine and H_2S (Khan et al. 2018; Li et al. 2019), which further amplify the physiological effect of H_2S. For instance, D/L-CDes, OAS-TL and CAS can be induced by H_2S under salt-alkali stress (Jiang et al. 2019; Kaya and Ashraf 2020; Li et al. 2020c). Low temperature stimulation can activate D/L-CDes and increase the content of endogenous H_2S (Aghdam et al. 2018; Fu et al. 2013). In addition to amplifying the signal of H_2S, the significant increase in endogenous H_2S content will further regulate the dynamic S metabolism in plants, thus promoting the production of sulfur derivatives (i.e., cysteine and GSH) and sulfur-containing proteins. H_2S can reduce the harm of heat stress by increasing the synthesis of total sulfhydryl compounds, proteins and cysteine in tobacco (*Nicotiana tabacum*) (Chen et al. 2019; Li and Jin 2016; Li et al. 2015b).

Under drought, salinity/alkali and heat stresses, the contents of chlorophyll and carotenoids in the leaves would decrease dramatically (Christou et al. 2013; Zhang et al. 2010b), as demonstrated by the decrease in potential photochemical efficiency (Fv/Fm), actual photochemical efficiency (ΦPSII), photochemical quenching (qP), electron transfer rate (ETR), and increase in non-photochemical quenching (qN). Intriguingly, these effects could be alleviated by NaHS (Li et al. 2015a). In addition, the enhancement of photosynthetic pigment, photosynthetic quantum yield, gas exchange parameters, SPAD value, and net photosynthetic rate (Pn) could also demonstrate the repair of photosynthesis by H_2S under toxic metal stress (Ahmad et al. 2020; Amooaghaie et al. 2017; Bharwana et al. 2014; Dawood et al. 2012; Fu et al. 2019; Kaya et al. 2018, 2020b; Kaya and Aslan 2020; Kushwaha and Singh 2020; Singh et al. 2015; Wang et al. 2020). For example, the expression of the D1 protein, a sensitive target of PSII damage, increased under drought stress. However, upon exposure to NaHS, less D1 protein and phosphorylated D1 protein were detected, which was putatively ascribed to the extra expression of *STN8* (catalyze D1 protein phosphorylation) and the genes related to D1 protein degradation, including *Deg1*, *Deg5*, *Deg8*, *FtsH2*, and *FtsH5*. These results suggest that H_2S alleviates drought-induced PSII damage owing to the fast turnover of D1 protein rather than its high content (Li et al. 2015a). Besides, higher light-saturated CO_2 assimilation rate (Asat), net photosynthetic rate (Anet), Fv/Fm and ΦPSII as well as the mRNA levels and activities of the key photosynthetic enzymes (Rubisco, TK, SBPase and FBA) were observed in H_2S-induced frost tolerance in cucumber (Liu et al. 2020c). In addition to the role in balancing redox homeostasis, H_2S may also promote the stability of chloroplast structure and photosynthesis, which will be discussed in the next section.

H_2S participates in drought stress response

For many plants in water shortage areas, multiple drought-tolerance mechanisms are essential, and H_2S has been identified as a new key factor in plant response to drought. In the early research, botanists found that the spraying of appropriate concentrations of NaHS could effectively improve the resistance of various plants to drought (García-Mata and Lamattina 2010; Zhang et al. 2010b). Such effects were observed in soybean (*Glycine max* L.), *Vicia faba*, wheat and *Arabidopsis* (Jin et al. 2011; Zhang et al. 2010b). Due to this broad-spectrum and beneficial physiological effect, later studies were mainly focused on two aspects: extensive exploration of the endogenous redox balance, ion homeostasis and H_2S-producing enzymes of plants, and investigation of the regulatory effect of H_2S on stomatal movement.

Water loss is the most intuitive effect of drought on plants. Water in plants evaporates into the air through stomata on the epidermis via transpiration. Therefore, the dynamic regulation of stomata is a significant index of plant water conservation. García-Mata and Lamattina (2010) first revealed the function of stomatal closure induced by H_2S in *Vicia faba, Arabidopsis* and *Impatiens walleriana*, and connected H_2S with ABA by treatment with H_2S scavenger (HT). With the suppression of endogenous H_2S, stomata would become less sensitive

to ABA in WT plants. However, Lisjak et al. (2010, 2011) reported that H_2S donor, NaHS and/or GYY4137, could promote stomatal opening of plants, which was ascribed to the reduction of NO accumulation in guard cells caused by H_2S. Similar work has been repeated in *Capsicum annuum*. This contradiction has raised some discussions (Desikan 2010). However, subsequent studies seemed to support the conclusion that stomatal closure is promoted by H_2S (Liu et al. 2011; Pandey 2014; Scuffi et al. 2016). Drought-induced hormone (i.e., ABA, salicylic acid (SA), jasmonic acid (JA) and ethylene) and ROS signals vary among plants, which promote the accumulation of H_2S in guard cells and initiate the signals downstream of H_2S to induce stomatal closure (Deng et al. 2020; García-Mata and Lamattina 2013; Jin et al. 2013; Liu et al. 2011; Scuffi et al. 2014). After that, the endogenous H_2S begins to exert its own functions, inducing the movement of guard cells indirectly by affecting the second messenger signals such as NO, H_2O_2, eATP, Ca^{2+}, phosphatidic acid (PA), carbohydrate, microfilament and microtubules, thus, promoting stomatal closure (Pantaleno et al. 2020). H_2S increases the content of NO in guard cells by activating NO-producing enzymes (García-Mata and Lamattina 2013), and the same effect was observed for H_2O_2. Recent experiments revealed that H_2S can increase the content of endogenous H_2O_2 in guard cells by promoting the production and enzyme activity of NADPH oxidase isoforms and phospholipase D isoforms (Scuffi et al. 2018), which is the most critical step to enhance the persulfidation level of NADPH oxidase isoforms, respiratory burst oxidase homolog D (RBOHD), and activate H_2O_2 synthesis (Shen et al. 2020). This process is related to the dynamic regulation of ROS by H_2S through its own chemical characteristic, and the regulation of a variety of secondary signal initiation enzyme systems by triggering S-persulfidation modification. H_2S can persulfidate DES1 and enhance its ability to produce H_2S, and then further persulfidates Open Stomata 1 (OST1)/SNF1-Related Protein Kinase2.6 (SnRK2.6) to accelerate the stomatal closure (Chen et al. 2020). Finally, on the one hand, H_2S directly or indirectly regulates the ion channels on the guard cell membrane, thus, changing the osmotic potential and turgor pressure of guard cells and resulting in stomatal closure. Using a non-invasive micro-test technique (NMT), it was found that endogenous H_2S induces a transmembrane K^+ efflux and Ca^{2+} and Cl^- influxes in guard cells, while not affects the flow of H^+ (Jin et al. 2017). Detection with two-electrode voltage clamp (TEVC) showed that H_2S selectively inhibits inward-rectifying K^+ channels of tobacco (*Nicotiana tabacum*) guard cells (Papanatsiou et al. 2015). In addition, H_2S also activates the S-type anion channel (SLAC1) in *Arabidopsis* guard cells with OST1 and cytosolic free Ca^{2+} (Wang et al. 2016). On the other hand, it can alter the morphology of guard cells by affecting the stability of cell membrane, cytoplasm and cell wall. H_2S inhibits the activities of polygalacturonase (PG) and endo-β-1,4-glucanase (EGase), thus, helping to maintain the integrity of cell wall in *Fragaria* × *ananassa* and *Actinidia deliciosa* (Gao et al. 2013; Zhang et al. 2014). H_2S also regulates the stability of microtubules by sulfhydryl actin and tubulin (Li et al. 2018a). Stable cell wall and cytoskeleton structure are essential for the movement of guard cells.

The advancement in omics studies provides a broader horizon of research. A total of 7552 transcripts have been investigated by transcriptome analysis. GO categories of 'transport' were enriched under the 'H_2S + drought' treatment, especially the ion transport categories. The KEGG pathways of 'ribosome biogenesis in eukaryotes', 'protein processing in endoplasmic reticulum', 'fatty acid degradation', and 'cyanoamino acid metabolism' were also induced by H_2S under drought stress (Li et al. 2017). In general, these results suggest that H_2S alleviates drought damage, which is probably related to transport systems, phytohormones signal transduction, protein-processing pathways, and metabolism of fatty acids and amino acids (Li et al. 2017). Similarly, using the isobaric tags for relative and absolute quantitation (iTRAQ) technique, 120 proteins were identified to be significantly regulated by NaHS under drought stress. Functional annotation revealed that nearly all 120 proteins are related to signal transduction, protein synthesis, carbohydrate metabolism, photosynthesis, stress, and secondary metabolism (Ding et al. 2018). Systematic analysis with different omics provides important guidance for future studies to dissect the mechanism for H_2S-dependent drought tolerance in plants.

H_2S boosts plant resistance to high salinity/alkali

High salinity and alkali conditions lead to osmotic stress and cell toxicity due to excess ions and ultimately nutrition disorders and oxidative stress in plants (Munns and Tester 2008), which will cause considerable yield losses. Recently, H_2S was recognized to play a key role in cell signaling during plant response to high salinity and alkali, even nitrate (Christou et al. 2013; Guo et al. 2018; Lai et al. 2014). H_2S can ameliorate salt-alkali stress-induced adverse effects (Jiang et al. 2019), which is partially similar to the case of other stresses, and the most distinctive feature is the reestablishment of redox balance (Lai et al. 2014). Besides, the

coordination of NO signal is indispensable for the preservation of a stable redox state by H_2S (Da-Silva et al. 2018; Janicka et al. 2018). H_2S not only increases endogenous NO and total S-nitrosothiols (SNOs) content in plants under salt-alkali stress (Christou et al. 2013; Ziogas et al. 2015), but also enhances the activity of nitrate reductase (NR) and glyoxalase I and II and decreases that of the S-nitrosoglutathione reductase (GSNOR) (Guo et al. 2018; Janicka et al. 2018; Mostofa et al. 2015). NO treatment can also elevate the content of H_2S and the activity of H_2S-producing enzymes. Similarly, exogenous NaHS and SNP can activate the enzyme activities for the rapid endogenous production of themselves (Ziogas et al. 2015).

Microarray analysis using GeneChip and proteomics analysis showed that nine functional categories consisting of thousands of genes had specific changes in salt-stressed seedlings after NaHS treatment, including metabolism, signal transduction, immune response, transcription factor, protein synthesis and degradation, transporter, cell wall decomposition and polymerization, hormone response, cell death, energy and unknown proteins (Guo et al. 2018; Li et al. 2014a, 2020c). Among them, the change in ion transporters is the most widely concerned. Another adverse effect of salt-alkali stress on plants is the breaking of ion balance, which is as serious as the oxidative burst. Salt stress can lead to the influx of a large amount of Na^+ into plant cells, which will directly destroy the membrane potential homeostasis on both sides of the cell membrane, and promote the outflow of intracellular K^+ (Zhang and Tielborger 2019; Zhu 2002). As observed in many plants, such as rice, wheat, strawberry, tomato, *Medicago sativa*, *Arabidopsis*, *Spartina alterniflora*, *Malus hupehensis*, *Populus euphratica* and *Populus popularis*, H_2S application can reduce the accumulation of intracellular Na^+ and the Na^+/K^+ ratio, and inhibit the exosmosis of intracellular K^+ (Ding et al. 2019; Guo et al. 2018; Lai et al. 2014; Li et al. 2020a, c; Mostofa et al. 2015; Wei et al. 2019; Zhao et al. 2018). On the one hand, H_2S increases the activity of PM H^+-ATPase under salt stress (Chen et al. 2015a; Jiang et al. 2019; Zhao et al. 2018), and induces the expression of several genes encoding the isoforms of the plasma membrane proton pump (*CsHA2*, *CsH4*, *CsH8*, *CsH9* and *CsHA10*) (Janicka et al. 2018). On the other hand, salt overly sensitive (SOS) pathway is activated by the up-regulation of related genes (i.e., *SOS1*, *SOS2*, *SOS3*, *SOS2-like*, *SOS3-like*, and *SOS4*) (Christou et al. 2013; Ding et al. 2019; Li et al. 2020a), which can effectively expel excessive Na^+ from the cells. Moreover, overexpression of SKORs and NSCCs and activation of mitogen-activated protein kinase (MPK) pathway also contribute to the rescue of plants by H_2S from salt stress (Deng et al. 2016; Jiang et al. 2019; Lai et al. 2014; Li et al. 2020a), which also restrain K^+ efflux in plant seedlings.

Systematic studies can help a better understanding of the downstream signal and mechanism for the alleviation effect of H_2S on salt-alkali stress. H_2S could promote photosynthetic electron transfer, chlorophyll biosynthesis and carbon fixation in *Kandelia obovata* leaves and cucumber under salt stress (Jiang et al. 2020; Liu et al. 2020d). In addition, the abundance of other proteins related to the metabolic pathways, such as antioxidation (APX, copper/zinc superoxide dismutase, pancreatic and duodenal homeobox 1), protein synthesis (heat-shock protein (HSP), chaperonin family protein 20 and Cysteine synthase 1), nitrogen metabolism (glutamine synthetase 1 and 2), glycolysis (phosphoglycerate kinase and triosephosphate isomerase), and the AsA-GSH cycle (glutathione S-transferase U25-like), was increased by H_2S under high salinity (Jiang et al. 2020; Liu et al. 2020d). However, the mechanism underlying the effect of H_2S on such huge proteins remains unclear (Guo et al. 2018; Li et al. 2014a, 2020c). Recent studies have revealed that H_2S signal acts on the downstream of transcription factors *VvWRKY30* and *JIN1/MYC2* under salt-alkali stress (Yastreb et al. 2020; Zhu et al. 2019). Hence, it remains to be explored whether there are any other transcriptional regulations or cascade regulations with hormone interference in the future.

H_2S helps to resist extreme temperature for plants

Extreme temperature is a severe limiting factor for the growth and productivity of plants (Iba 2002; Suzuki 2019; Wu and Wallner 1984). Different from animals, plants are lack of movability to evade from harmful circumstances. To cope with extreme circumstances, plants have evolved certain effective regulatory mechanisms. H_2S is involved in the complex regulatory network of plants to resist extreme environmental temperature.

Damages caused by heat exposure include protein denaturation and aggregation, membrane damage owing to lipid peroxidation, enzyme inactivation, inhibition of protein synthesis, imbalance of redox hemostasis and secondary metabolic disorder (Carmody et al. 2016; Posch et al. 2019; Proveniers and van Zanten 2013). Meanwhile, plants can initiate self-help operations to alleviate the damage caused by high temperature. During this process, the contents of endogenous NO and H_2S would be significantly increased, which is largely dependent on the increased expression and initiated activity of the relevant enzymes (Cheng et al.

2018; Li et al. 2013b; Ye et al. 2020). Interestingly, SNP-induced heat tolerance of maize was enhanced by the application of H_2S donors (Li et al. 2013b). It seems that H_2S acts on the downstream of NO-induced heat tolerance in maize seedlings. Besides, the addition of NaHS leads to dramatic increases in AsA, GSH, flavonoids and carotenoids in maize (Ye et al. 2020). H_2S induces the accumulation of endogenous Pro, due to higher Delta (1)-pyrroline-5-carboxylate synthetase (P5CS) activity and lower proline dehydrogenase activity (Li et al. 2013a). H_2S also activates trehalose-6-phosphate phosphatase (TPP) and betaine aldehyde dehydrogenase (BADH), and then induces the accumulation of endogenous trehalose and betaine under heat stress (Li et al. 2014d; Li and Zhu 2015). Furthermore, H_2S pretreatment also induced the gene expression levels of an array of protective molecules, such as heat shock proteins (*HSP70*, *HSP80*, and *HSP90*) and aquaporins (*PIP*) (Christou et al. 2014).

Together with H_2S, exogenous Ca^{2+} and CaM can effectively alleviate the damage to plants caused by high temperature stress partly via strengthening the L-CDes activity and H_2S accumulation (Li et al. 2015c). The acquisition of H_2S-induced heat tolerance requires the transport of extracellular Ca^{2+} to cytoplasm and the coordination of intracellular CaM (Li et al. 2012c). Methylglyoxal (MG), which is viewed as a toxic by-product of glycolysis and photosynthesis in plants and resembles H_2S, participates in the response to abiotic stress. Similar to the scenario of Ca^{2+} and H_2S, application of MG and/or NaHS enhanced the survival and tissue vigor of maize seedlings under heat stress (Li et al. 2018b; Ye et al. 2020). Obviously, there is an interaction between H_2S and MG that initiates the thermotolerance in plants. Furthermore, some traditional signals in the regulation of heat-tolerance mechanism also have crosstalk with H_2S signals, such as CO, ABA and SA (Li and Gu 2016; Li and Jin 2016; Li et al. 2015d), which can sequentially induce the activation of H_2S-producing enzymes and accumulation of endogenous H_2S under high-temperature stress.

Low temperature is another extreme temperature condition. Long-term frosty weather affects agricultural production and operations (Furtauer et al. 2019). H_2S fumigation can significantly increase the activity of H^+-ATPase, Ca^{2+}-ATPase, cytochrome C oxidase (CCO) and succinate dehydrogenase (SDH) related to energy metabolism (Li et al. 2016a). NaHS treatment also increased the content of anthocyanins in wheat seedlings and cucurbitacin C (CuC) in cucumber (Kolupaev et al. 2019; Liu et al. 2019c). The latter may be due to the increase in the S-persulfidation level of bHLH transcription factors (*His-Csa5G156220* and *His-Csa5G157230*) caused by H_2S, as well as their binding activity to the promoter of the key synthetase Csa6G088690 for CuC fabrication (Liu et al. 2019c). H_2S also amplifies the signal transmission induced by cold via regulating the transcription of genes, such as *VvICE1* and *VvCBF3* genes in *Vitis vinifera* (Fu et al. 2013). In *Arabidopsis*, H_2S up-regulates MAPK expression levels, and both H_2S and MPK4 regulate the expression levels of the cold responsive genes *inducer of CBF expression 1* (*ICE1*), *C-repeat-binding factors 3* (*CBF3*), *cold responsive 15A* (*COR15A*) and *COR15B* (Du et al. 2017). This result suggests that MPK4 is probably a downstream component of H_2S-related cold-stress resistance, which links the H_2S signal with the classical cold signal regulated by MAPKs.

H_2S rescues plants from hypoxia and waterlogging

Flooding often results in hypoxic conditions around plant roots, which is a serious stress to crops. As hypoxia is the most important consequence of flooding stress, it will be discussed in this section as well. Submerging in water can cause stress to most terrestrial plants, which can result in low availability of light, CO_2 and oxygen and hence pose challenges to the normal functions of the plant system (Pandey and Gautam 2020). Flooding increases the emissions of some trace gases such as N_2O, N_2, CH_4 and H_2S in the environment around the crops (Kogel-Knabner et al. 2010).

When confronted with the adverse effects caused by hypoxia, plants will carry out some rescue activities. One possibly way is to increase the endogenous H_2S content by enhancing the activities of H_2S-related enzymes (Cheng et al. 2013; Peng et al. 2016). Exogenous application of low H_2S in *Pisum sativum* and peach can reverse ROS accumulation, cell deaths, electrolyte permeability, rapid synthesis of ethylene and significant reduction of root activity that induced by waterlogging stress (Cheng et al. 2013; Xiao et al. 2020). In addition, there is also a similar relationship between AsA-GSH cycle and H_2S (Shan et al. 2020). The mode is similar to that under osmotic stress, which has been introduced in the above section. Hypoxia stress can lead to cell apoptosis, which is related to ethylene synthesis, and there is a parallel relationship between ethylene synthesis and excessive accumulation or apoptosis (Peng et al. 2016). Jia et al. (2018a) showed that H_2S reduces ethylene production by inhibiting the activity of 1-aminocyclopropane-1-carboxylic acid (ACC) oxidases (ACOs). H_2S induces the persulfidation of LeACO1 and $LeACO_2$ in a dose-dependent manner, thus, inhibiting the activity of LeACO1 and LeACO2 (Jia et al. 2018a).

These results provide insights into the general action mode of H_2S and contribute to a better understanding of a plant's response to hypoxia and waterlogging stress.

H_2S responses to toxic metal stress

Heavy metals, such as copper (Cu), mercury (Hg), lead (Pd), Cd, arsenic (As), chromium (Cr) and zinc (Zn) (Luo et al. 2020), will cause chronic poisoning when accumulated to a certain extent in organisms. Due to its similar toxicity, Al is also included, and these metals are collectively referred to as toxic metals. Here, we systematically review whether and how H_2S alleviates toxic metal stress in plants (Table S1).

Toxic metal stress can increase the death of plant somatic cells as well as reduce survival rate, biomass and yield of crops (Ahmad et al. 2020; Fu et al. 2019; Kaya et al. 2018, 2020b; Kaya and Aslan 2020), which are attributed to the destruction of endogenous redox balance and excessive accumulation of ROS. Exogenous H_2S alleviates the stress of toxic metals and improve the survival rate and biomass of plant seedlings, which is also due to the remodeling of the stable redox state by H_2S in plants. Notably, this will also increase the species and quantity of microorganisms in the rhizosphere soil (Fang et al. 2019).

Some toxic metals, such as Cu, Co, Cr and Cu, are originally the micronutrients essential for plants, especially in the photosynthetic system, which are involved in the composition of pigments and coenzymes. However, excessive toxic metals will directly destroy the photosynthetic system and organelles in plant cells (Singh et al. 2015). In *Brassica* and barley, toxic metals could destroy the stability of chloroplast structure in mesophyll cells, making the chloroplasts spongy, increasing thylakoid solvents and starch, and leading to the breakage of other organelles in root, stem and leaf cells (Ali et al. 2013; Qian et al. 2014; Shi et al. 2014). After the application of H_2S, increases in the number of mature mitochondria, long endoplasmic reticulum and Golgi bodies could be observed in plant cells (Ali et al. 2014; Qian et al. 2014).

Another mechanism for H_2S to alleviate toxic metal stress is to enhance the fixation of toxic metal ions, which is closely associated with the function of cell wall, the regulation of transporters, as well as the cooperation of plant chelators and other signals. Cell wall, the unique structure of plant cells, can bind and fix Cd ions from the extracellular environment to alleviate its toxicity. Exogenous H_2S can significantly increase the content of pectin and the activity of pectin methylesterase in *Brassica* roots, thereby increasing the retention of Cd in pectin fractions (Yu et al. 2019). However, when rice was subjected to Al stress, H_2S pretreatment reduced the negative charge in cell walls by decreasing the activity of pectin methylesterase as well as the pectin and hemicellulose contents in roots (Zhu et al. 2018). Plant cells can also alleviate the toxicity by transporting toxic metal ions into vacuoles, which is dependent on the action of H^+-ATPase and citrate transporters on the vacuole membrane. This effect will be amplified by the application of H_2S, and enhancement of the expression and activity of tonoplast H^+-ATPase could reduce cytoplasmic toxic metal ions, which has been reported in crops such as *Populus euphratica* (Cd^{2+}/H^+ antiporters), soybean (H^+-ATPase) and barley (Na^+/K^+-ATPase and W-ATPase) (Chen et al. 2013; Dawood et al. 2012; Sun et al. 2013; Wang et al. 2019). Induction of soybean *GmMATE13*, *GmMATE47* and rice *OsFRPL4* by H_2S could alleviate Cd and Al stress by increasing citrate exudation (Chen et al. 2013; Yu et al. 2019; Zhu et al. 2018). Under Al stress, rice *OsNRT1* and *OsALS1* were also induced by H_2S, which reduced the content of Al in cytoplasm by transferring Al to vacuoles (Zhu et al. 2018). The most effective strategy for plants to cope with the threat of toxic metals is to temporarily "inactivate" the metal ions through GSH phytochelatins (PCs) and metallothionein (MTs), which is closely related to the sulfur metabolism pathway with H_2S-cysteine as the core. Even without exogenous H_2S, toxic metal stress can induce the activity of CDes, OAS-TL, CAS and SATs (Cui et al. 2014; Fang et al. 2016, 2017; Jia et al. 2016, 2018b; Lv et al. 2017; Talukdar 2015; Yu et al. 2019), resulting in the production of more endogenous H_2S and cysteine (Jia et al. 2016; Shi et al. 2014; Talukdar 2016; Zhang et al. 2010a). Cysteine is the raw material for GSH synthesis through γ-CEs synthetase and GSH synthase (Jobe et al. 2012), and H_2S can increase the expression of the genes related to PCs and MTs through transcriptional regulation (Fang et al. 2014a, 2016; Jia et al. 2016; Liu et al. 2016; Valivand et al. 2019a).

There are certain correlation relationships of other signals with H_2S under toxic metal stress. NO, the principal partner of H_2S, is also endogenously synthesized in response to toxic metal stress just like H_2S (Shi et al. 2014). Exogenous application of SNP has a similar action mode to NaHS in alleviating toxic metal stress (He et al. 2019; Zhu et al. 2018), which may be related to the interaction between H_2S and NO in the regulation of redox balance (Shivaraj et al. 2020). Ca^{2+} also assists H_2S to alleviate toxic metal stress. Some divalent metal ions, such as Cd^{2+}, Mn^{2+} and Ga^{2+}, can block the activity of calcium channels in plants, and Ca^{2+} can also mediate the detoxification process (Fang et al. 2017). For example, CDPK3 could enhance LCD activity in

Arabidopsis, and the content of GSSH (S-persulfidation) was significantly lower in *lcd* and *cdpk3* mutants (Qiao et al. 2016). Interestingly, seed priming with NaHS increased the CDPK transcripts in seedling leaves of zucchini under Ni stress (Valivand et al. 2019a, b). In addition, the signals to alleviate toxic metal stress by regulating the synthesis of H_2S also include plant hormones (SA, ABA), gas molecules (SO_2, H_2), elements (Si) and some special organic compounds (Thiamine, Eugenol) (Hu et al. 2018; Kaya et al. 2020a; Kaya and Aslan 2020; Qiao et al. 2015; Zanganeh et al. 2019; Zhu et al. 2015). All of them have been reported to activate the H_2S response pathway by increasing the activity of H_2S-producing enzymes or endogenous H_2S level (Hu et al. 2018; Kaya et al. 2020a; Kaya and Aslan 2020; Qiao et al. 2015; Zanganeh et al. 2019; Zhu et al. 2015). However, cinnamaldehyde was found to alleviate the toxic metal stress in a different action mode, which inhibits the activity of D-CDes in tobacco, and thus, reduces the content of endogenous H_2S (Ye et al. 2017).

Recently, the regulatory pattern of trans-acting factors in the promoter region of key genes for H_2S synthesis has been reported. WRKY18 and WRKY60 bind to the motif W-box in the promoters of LCD, DCD1, DCD2, DES and NFS2, and WRKY40 binds to the same motif of NFS1. The mRNA levels of the *LCD, DES* and *DCD1* genes were up-regulated, but that of *DCD2* was down-regulated in *wrky18*, *whky40* or *wrky60* mutants (Liu et al. 2015). Another WRKY family gene, *WRKY13*, is induced by Cd and thus activates DCD expression to increase the production of H_2S (Zhang et al. 2020). Similarly, bZIP transcription factor TGA3 enhances the production efficiency of H_2S via combining with the LCD promoter in response to Cr (VI) stress. Ca^{2+}/CaM2 physically interacts with TGA3 to enhance the binding of TGA3 to the LCD promoter (Fang et al. 2017).

Roles of H_2S in biotic stress response

Sulfur fertilization can enhance the resistance of crops against fungal pathogens. It was found to obviously increase the contents of total S, sulfate, organic S, cysteine, and GSH in *Brassica*, but decrease the L-CDes activity (Bloem et al. 2004). Moreover, infection with *Pyrenopeziza brassicae* increased the cysteine and GSH contents and the L-CDes activity (Bloem et al. 2004). Exposure to fungal infection is accompanied by increased emissions of S-containing gases, including H_2S and COS (Bloem et al. 2011, 2012).

Exogenous NaHS can effectively inhibit the merisis of pathogenic bacteria and cure plant diseases. For example, fumigation with H_2S could inhibit spore germination, mycelial development and pathogenicity of *Monilinia fructicola* in peach fruit (Wu et al. 2018), and also significantly inhibited the two fungal pathogens of pear, *Aspergillus niger* and *Penicillium expansum* (Tang et al. 2014). These results suggest that H_2S can enhance the resistance of plants to pathogen infection, and the production of endogenous H_2S is induced by immune signal and exogenous sulfide.

It is interesting to know how H_2S helps to resist pathogenic microorganisms as an immune substance in plants. A study on *Escherichia coli* found that NaHS treatment stimulated the production of ROS and decreased the GSH level in *E. coli*, resulting in lipid peroxidation and DNA damage (Fu et al. 2018a). Meanwhile, H_2S inhibits the antioxidative enzyme activities of SOD, CAT and GR and induces the response of the SoxRS and oxyR regulons in *E. coli*, which is contrary to the antioxidant pattern of H_2S in plants (Fu et al. 2018a). Hu et al. (2014b) isolated three fungal pathogens, including *Rhizopus nigricans*, *Mucor rouxianus* and *Geotrichum candidum*, from sweetpotato infected with black or soft rot. H_2S fumigation greatly reduced the percentage of fungal infection upon the inoculation of these three fungi on the surface of sweetpotato slices (Tang et al. 2014). It is marvelous that some pathogens have even evolved certain response mechanisms for resistance against the toxicity of H_2S emitted by plants. Plant pathogens *Xylella fastidiosa* and *Agrobacterium tumefaciens* employ the *BigR* operon, which is regulated by the transcriptional repressor *BigR* and encodes a bifunctional sulfur transferase and sulfur dioxygenase enzyme, to oxidize H_2S into sulfite (De Lira et al. 2018). In a feedback mechanism, H_2S and polysulfides inactivate *BigR* and then initiate operon transcription (De Lira et al. 2018). However, the participation of H_2S in plant resistance to pathogenic microorganisms is much more complex than what has been known, which is also a field worthy of exploration with interdisciplinary.

H_2S CONTRIBUTES TO PLANT GROWTH AND DEVELOPMENT

H_2S is also involved in regulating the growth and development process in plant life cycles (Li et al. 2016b). Here, we summarize the existing findings to provide a better understanding on how H_2S affects the growth and development of plants.

H_2S promotes seed germination

Seed germination is the most critical and flimsy phase of plant life cycle because of its high vulnerability to injury,

disease and environmental stress (Rajjou et al. 2012). Recently, a number of studies have elucidated that H_2S is involved in the process of seed germination. H_2S may promote germination by alleviating the adverse effects of multiple stresses on the seeds. For instance, exogenous NaHS could alleviate the toxic metal stress of wheat seeds (Hu et al. 2015b; Zhang et al. 2010c), the osmotic stress of cucumber seeds (Mu et al. 2018), the high temperature stress of maize seeds and the salinity stress of alfalfa and wheat seeds (Chen et al. 2019; Wang et al. 2012; Zhou et al. 2018). The related mechanisms have been discussed in detail in the previous section. Here, we will focus on the promotion effect of H_2S on plant seed germination without stress. H_2S affects seed germination in a dose-dependent manner, but too high concentration will lead to inhibition of germination (Baudouin et al. 2016). For cucumber seeds, the germination energy and efficiency and the seedling growth were promoted by H_2S (Mu et al. 2018). In bean, corn, wheat, and pea, H_2S can increase the germination rate and seedling size and shorten the germination time (Dooley et al. 2013a). Interestingly, endogenous H_2S content is enhanced in germinating seeds without exogenous S fertilizer. The increase in H_2S is associated with higher activity of D/L-CDes and CAS (Baudouin et al. 2016). Purification and biochemical characterization of CAS expressed in germinating seeds of *Sorghum bicolor* again confirmed that high CAS activity promotes seed germination (Amiola et al. 2018). However, NaHS treatment was ineffective in breaking seed dormancy since the germination of *des1* and WT seeds was inhibited by ABA to almost the same degree (Baudouin et al. 2016). Surprisingly, H_2O_2 can also promote seed germination, indicating that H_2O_2 and H_2S can synergistically promote seed germination. Soaking with H_2O_2 greatly improved the germination rate of *Jatropha curcas* seeds by stimulating the L-CDes activity, which in turn induced the accumulation of H_2S (Li et al. 2012b). Conversely, NaHS treatment increased the contents of endogenous H_2S and H_2O_2 in germinating seeds, and the accumulation of H_2O_2 lagged behind that of H_2S, indicating that H_2S acts upstream of H_2O_2 in seed germination of mung bean (Li and He 2015). Either H_2S or H_2O_2 can dramatically stimulate protease activity and production of total free amino acids in cotyledons. These results suggest that both H_2S and H_2O_2 can promote the seed germination of mung bean via mobilizing the storage protein. Actually, the mechanism for the effect of H_2S on seed germination still remains elusive. Plant hormone crosstalk, DNA repair, protein PTMs, metabolite synthesis and mRNA transcription are all potentially responsive to H_2S signaling.

Dual effects of H_2S on root development

H_2S shows dual regulatory effects on root development: it promotes root growth at low concentrations but inhibits root growth at high concentrations. In the previous experiments of our group, *Arabidopsis* grown on 1/2 MS medium supplemented with 10 ∼ 100 μmol/L NaHS had longer roots than the control, while NaHS at concentrations over 200 μmol/L inhibited root elongation, and even suspended root elongation when the concentration exceeded 2 mmol/L. Exogenous application of low concentrations NaHS was found to promote the activity of L-CDes in root cells (Fang et al. 2014c; Hu et al. 2020a), thus, increasing the content of endogenous H_2S, which would directly promote the development and growth of roots. The same phenomenon was also observed in strawberry seedlings (Hu et al. 2020a). Specific fluorescent probe WSP-1 was applied to track endogenous H_2S in tomato roots in site, and the results further confirmed that H_2S accumulation is associated with primordium initiation and lateral root emergence (Li et al. 2014c). Furthermore, fluorescence tracking of endogenous H_2S in situ showed that H_2S was accumulated exclusively in the outer layer cells of the primary root where lateral roots emerged (Xue et al. 2016). Pharmacological and biochemical approaches were combined to investigate the crosstalk among H_2S, NO, CO, indole acetic acid (IAA) and Ca^{2+} in regulating the development and growth of roots. A rapid increase in H_2S and NO was sequentially observed in shoot tips of sweet potato seedlings treated with NaHS. However, the induction effect of H_2S on root growth was eliminated by *N*-1-naphthylphthalamic acid (NPA), an IAA transport inhibitor, and 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO), an NO scavenger (Zhang et al. 2009). Fang et al. (2014b) observed that down-regulation of *SlDES* induced by auxin depletion would decrease DES activity and endogenous H_2S content, and inhibited lateral root formation. Conversely, treatment with NAA or NaHS could induce endogenous H_2S, and thereafter stimulate lateral root formation in the same mode. Subsequently, both NaHS- and NAA-regulated modulation genes of cell cycle, including the up-regulated *SlCDKA;1* and *SlCYCA2;1*, together with the down-regulated *SlKRP2*, were reversed by HT pretreatment (Fang et al. 2014b). Notably, these results suggest that H_2S is a downstream component of auxin signaling to trigger lateral root formation.

For oxidation signals, NO and CO promote root growth similarly to H_2S at low concentrations. Exogenous application of NaHS and the heme oxygenase-1 (HO-1) inducer hemin induced lateral root formation in

tomato seedlings by triggering intracellular signaling events that involve the induction of tomato HO-1 and the modulation genes of cell cycle, including the up-regulation of *SlCDKA;1* and *SlCYCA2;1* and down-regulation of *SlKRP2* (Fang et al. 2014c). Hence, HO-1/CO might be involved in H_2S-induced lateral root formation in tomato. SNP could stimulate the generation of endogenous H_2S and the expression of related enzyme genes. HT or PAG partially block the SNP-induced formation of lateral roots and the expression of lateral root-related genes (Li et al. 2014c). Deficiency of H_2S could abolish the stimulatory effect of NO on intracellular Ca^{2+} and *CAM1* transcription levels. Moreover, Ca^{2+} chelator or Ca^{2+} channel blocker diminished H_2S-induced formation of lateral roots (Li et al. 2014c). These findings indicate that the interaction of H_2S and Ca^{2+} signal is downstream of NO signal in the process of promoting root development. In addition, the effect of methane (CH_4) on root growth and development was also found to be related to H_2S signal, which is also the case for CA (Xue et al. 2016). Exogenous CH_4 increased the endogenous H_2S level by stimulating the activities of corresponding enzymes, and thus induced the expression of *CsDNAJ-1*, *CsCDPK1*, *CsCDPK5*, *CsCDC6* (a cell-division-related gene), *CsAux22D-like* and *CsAux22-like* (two auxin-signaling genes) (Kou et al. 2018). Recent research has further confirmed the relation between CH_4 and H_2S, along with the advancement in transcriptional profiling analysis, increasing representative cell cycle regulatory genes, miRNA and their target genes have been identified, which are mostly involved in the promotion of root development by CH_4 and H_2S (Mei et al. 2019).

H_2S may also act as an inhibitory signal of plant root development and growth at high concentrations in the environment. In this case, there are different regulatory mechanisms compared with the abovementioned pathways. High H_2S inhibits the elongation of primary roots by inhibiting the transport of auxin (Jia et al. 2015). Vesicle trafficking and distribution of the PIN proteins are an actin-dependent process, whereas H_2S alters the polar subcellular distribution of PIN proteins by controlling the expression of several actin-binding proteins (ABPs) and suppressing the occupancy percentage of filamentous actin (F-actin) bundles in *Arabidopsis* roots, which eventually inhibits auxin polar transport (Jia et al. 2015). In addition, the effects of H_2S on F-actin are partially depleted in T-DNA insertion mutants *cpa*, *cpb* and *prf3*. The density of F-actin bundles and the F-actin/globular actin ratio are lower in overexpressing LCD/OASA1 lines (Li et al. 2018a). Besides, actin protein ACTIN2 (ACT2) is persulfidated at Cys-287, which is adjacent to the D-loop, a core region for hydrophobic and electrostatic interactions, and stabilizes F-actin filaments (Li et al. 2018a). A high accumulation of H_2S results in the depolymerization of F-actin bundles and then inhibits root hair growth. Furthermore, a high concentration H_2S represses primary root growth by triggering a signal transduction pathway involving ROS burst, MPK6 activation, and NO accumulation (Zhang et al. 2017). Exogenous H_2S-induced ROS production is required for NO generation, and MPK6 mediates H_2S-induced NO production, suggesting that MPK6 acts downstream of ROS and upstream of NO (Zhang et al. 2017). It remains to be determined whether these vital signals related to the subcellular localization of auxin are inhibited by H_2S in the future.

Functions of H_2S in photosynthesis and photomorphogenesis

When plants suffer from various abiotic stresses, the imbalance of redox state and the disorder of ion transport will largely restrict the photosynthesis of plants. Exogenous H_2S can promote photosynthesis with a higher chlorophyll content in a variety of plants (Chen et al. 2015b; Liu et al. 2020b; Parveen et al. 2017), even in lower algae (Dooley et al. 2013b, 2015; Joshi et al. 2020), suggesting that the promotion of H_2S on plant photosynthesis appeared in a very early period of plant evolution to improve plant survival. Chen et al. (2011) have revealed the role of H_2S in photosynthesis in *Spinacia oleracea*. Besides increasing the chlorophyll content, NaHS treatment also promotes seedling growth, soluble protein content, photosynthesis and stacked number of grana lamellae; similarly, the light saturation point (Lsp), maximum net photosynthetic rate (Pmax), carboxylation efficiency (CE), and Fv/Fm all reached their maximal values, whereas the light compensation point (Lcp) and dark respiration (Rd) decreased significantly under NaHS treatment (Chen et al. 2011). H_2S also enhances the activity of ribulose-1,5-bisphosphate carboxylase (RuBISCO) and the protein expression of the RuBISCO large subunit, as well as OAS-TL and L-CDes (Chen et al. 2011). Furthermore, H_2S positively influences the growth and physiology of rice, including photosynthesis, photorespiration, chlorophyll fluorescence, and stomata. H_2S treatment reduced the photosynthesis oxygen sensitivity, CO_2 compensation point and glycolate oxidase (GOX) activity, and increased the photosynthetic rate and stomatal conductance (Duan et al. 2015). A recent study revealed that the deletion of either OASB or SERAT2;1 frequently induced antagonistic alterations in biochemical or molecular features (Muller et al. 2017). All of these findings indicate that H_2S and the related S metabolism are

important for chloroplast photosynthesis and related functions.

It is noteworthy that except for participation in the photosynthetic system from multiple perspectives, the relationship between H_2S and light is also reflected in the perception of light signals, plant photomorphogenesis, and even the alleviation of light stress. Exogenous H_2S can effectively alleviate the photoinhibition of *Dendrobium officinale* (Fan et al. 2014). Intriguingly, a similar mode of enhancement occurs in plants at a low light availability (Liu et al. 2019a). Plant photosynthesis is dependent on the plant's perception of light and related signal transduction. H_2S was also found to act downstream of plant light signal, which is induced by light in a specific band. In seedlings of foxtail millet, the H_2S content in the hypocotyl increased initially under red, blue or white light, and the duration of increase under white light was longer than that under red or blue light (Liu et al. 2019b). The activity of CDes was increased by red light but decreased by blue and white light. The expression of *LCD1* and *LCD2* was promoted by red or white light, but inhibited by blue light (Liu et al. 2019b). In contrast, the *DES* gene was promoted by white light but inhibited by red or blue light. In addition, the activities of LCDs were regulated by the phosphorylation under the mediation of photoreceptors PHYB and CRY1/CRY2 (Liu et al. 2019b). These findings suggest that there are two ways to regulate the production of H_2S in light-signaling network: a rapid pattern that involves the phosphorylation occurring on LCDs protein directly or indirectly mediated by photoreceptors, and a slow pattern that involves the regulation of mRNA transcription of *LCDs* and *DES* genes. As for photomorphogenesis, H_2S promotes the elongation of hypocotyls. NaHS treatment blocked the efflux of the E3 ligase constitutive photomorphogenesis 1 (COP1) from nucleus to cytoplasm and increased the degradation of elongated hypcotyl 5 (HY5), thereby boosting the development of plants by inhibiting the expression of *ABI5* (Chen et al. 2019). At present, little is known about whether H_2S is involved in photosynthesis, photomorphogenesis or light signal transduction. Considering the importance of photosynthesis in a broad sense, it is promising to carry out in-depth research on H_2S function.

H_2S resists aging and programmed cell death

The function of H_2S in alleviating cell senescence and apoptosis has been widely studied in mammalian cells, such as vascular endothelial cells (Das et al. 2018), neuronal cells (Wu et al. 2019), kidney cells (Chen et al. 2018), and tumor cells (Szadvari et al. 2019). Similar phenomena were observed in plants. Many external factors, such as damage (Zhang et al. 2011), hormone induction (Xie et al. 2014a), and lack of light (Hu et al. 2015a; Li et al. 2015e), can lead to early senescence in plants. Besides, rhythm, climate and seasonal changes also induce the natural aging of plants. It is miraculous that H_2S is involved in these signals and reverses this natural process. Exogenous application of NaHS could significantly prolong the survival time of various cut flowers (Zhang et al. 2011), leaves and fruits in vitro (Hu et al. 2015a; Liu et al. 2017), by maintaining the stability of pigment content as well as reducing the respiration rate, oxidative damage and the subsequent PCD process in plant cells. Over accumulation of ROS can induce autophagy in plant cells, and the scavenging ability of H_2S on ROS through antioxidant enzymes is dependent on the increase in both transcription and enzyme activities. Naturally, H_2S weakens the aging promoting effect of ROS.

For example, H_2S treatment alleviated dark-promoted senescence in broccoli florets by sustaining higher activities of GPX, APX, CAT and GR and lower activities of lipoxygenase (LOX), PPO, PAL and protease (Li et al. 2014b, 2015e). Similarly, NaHS treatment on aleurone tissue led to higher transcript levels of the antioxidant genes *HvSOD1*, *HvAPX*, *HvCAT1* and *HvCAT2* and lower transcript levels of *HvLOX* and cysteine protease genes *HvEPA* and *HvCP3-31* (Zhang et al. 2015a). Exogenous H_2S can increase the contents of chlorophyll, carotenoids, anthocyanins and ascorbate through metabolic pathways, and down-regulate the transcription of genes related to chlorophyll degradation (*BoSGR*, *BoCLH2*, *BoPaO*, and *BoRCCR*), thus inhibiting the etiolation process (Hu et al. 2015a; Li et al. 2014b, 2015e). Hormones such as GA and ethylene can induce aging, and H_2S can counteract their signals through potential antagonism. In wheat aleurone cells, H_2S alleviates GA-induced PCD via resuming the production of H_2S, increasing the content of GSH and NO and the expression of HO-1 and α-amylase (Xie et al. 2014a; Zhang et al. 2015a). The role of GSH in alleviating autophagy has been reported previously in mammalian cells. For example, the deletion of *GCLM*, a GSH synthesis-related gene, could cause premature aging of fibroblasts and ovarian cells (Chen et al. 2009; Lim et al. 2013). The role of NO in alleviating plant senescence has also been systematically reviewed (Gotor et al. 2013). Meanwhile, D/L-cysteine and H_2S can delay the aging time of parsley and peppermint by decreasing ethylene synthesis (Al Ubeed et al. 2019).

Another way to delay aging by H_2S is to reduce the respiratory rate and restore and enhance the energy metabolism. H_2S can alleviate autophagy induced by

carbon starvation (Álvarez et al. 2012). Subsequently, H_2S was found to delay senescence by maintaining the energy status in plants (Liu et al. 2017). In *Arabidopsis*, the mitochondria of *des1* were severely damaged and bubbled in older leaves, while OE-DES1 had complete mitochondrial structures and a homogeneous matrix (Jin et al. 2018). In addition, mitochondria isolated from OE-DES1 showed significantly higher H_2S production rate, H_2S content and ATPase activity level, as well as lower levels of swelling and ATP content compared with the WT and *des1* (Jin et al. 2018). Besides, the decrease in H_2S caused by DES1 deletion also inhibited the expression of *ATPβ-1, 2, 3,* while induced that of *ATPε* (Jin et al. 2018). At the transcriptional level, H_2S delays the aging process by regulating senescence-related genes. For instance, H_2S alleviates the aging of foliar cells by inhibiting the expression of *SAG13*, *ATG8b* and *ATG12a* while inducing that of *SAG12* (Álvarez et al. 2012; Jin et al. 2018; Wei et al. 2017). Recently, it was found that H_2S inhibited the abscission of the tomato petiole in a dose-dependent manner, and up-regulated the expression of *SlIAA3* and *SlIAA4* but down-regulated that of *ILR-L3* and *ILR-L4* in the earlier stages of the abscission process (Liu et al. 2020a). Moreover, proteomic analysis under ABA treatment showed that persulfidation of the cysteine protease ATG4 could regulate autophagy in *Arabidopsis*. H_2S-induced persulfidation of ATG4 protease directly promotes the post-translational processing of ATG8, which negatively regulates the progress of autophagy (Laureano-Marín et al. 2020). It should also be noted that the action mode for SO_2 to alleviate plant senescence is just like that of H_2S (Sun et al. 2018; Wang et al. 2017), indicating that the relation between SO_2 and H_2S is established through the thiometabolism pathway.

H_2S delays fruit ripening and prolongs postharvest freshness

Application of H_2S donor NaHS or Na_2S could significantly inhibit the decay and mildew of postharvest fruits, and prolong their storage time (Ali et al. 2019; Mukherjee 2019; Ziogas et al. 2018). Exogenous H_2S can regulate the redox balance, hormone level, thiometabolism and energy metabolism in fruits, maintain the homeostasis of various secondary metabolites and the integrity of cell wall and cell membrane, as well as help to resist the invasion of a variety of fungi by inhibiting the mycelial germination (Table S2).

As mentioned above, H_2S can significantly enhance the activities of antioxidant enzymes, including CAT, SOD, APX and POD (Aghdam et al. 2018; Gao et al. 2013; Hu et al. 2012, 2014a; Luo et al. 2015; Yao et al. 2018). Interestingly, the mechanisms by which H_2S regulates redox balance are complex and diverse in different fruits. In the fruits of strawberry, kiwifruit, pear and sweet potato, H_2S inhibits the oxidation of lipids by reducing the activity of LOX (Gao et al. 2013; Hu et al. 2012, 2014b; Tang et al. 2014). H_2S fumigation was found to inhibit the activities of PAL and PPO in apple, banana, tomato and pear fruits (Hu et al. 2014b; Luo et al. 2015; Yao et al. 2018; Zheng et al. 2016). Phenolic compounds are maintained at low levels, which also helps to prevent the oxidative browning of fruits such as lotus root, apples and pears after cutting (Hu et al. 2014b; Sun et al. 2015; Zheng et al. 2016). H_2S can also improve the activity of GR in strawberry fruit (Hu et al. 2012) and kiwi fruit (Gao et al. 2013). Aroca et al. (2015) revealed that H_2S can directly enhance CAT activity in *Arabidopsis* through S-persulfidation. Liu et al. (2017) pointed out that H_2S enhances the activities of SOD, CAT and APX in *Hemerocallis Liliaceae*, among which APX may be directly regulated by H_2S-induced persulfidation. In most cases, H_2S enhances the activity of antioxidant enzymes. Moreover, H_2S also increases the expression of *SlAPX2*, *SlCAT1*, *SlPOD12* and *SlCuZn-SOD* genes in tomato (Yao et al. 2018). These findings indicate that H_2S regulates ROS not only through PTM, but also at the transcriptional level (Begara-Morales et al. 2014; Palma et al. 2020).

Exogenous H_2S also affects different secondary metabolic processes. For sulfide and sulfate metabolism, H_2S enhances the activity of D/L-CDes, and thus increases the content of endogenous H_2S in fruits (Aghdam et al. 2018; Hu et al. 2014a; Liu et al. 2017; Munoz-Vargas et al. 2018). The sugar/acid ratio of plant fruit is considered as an important index of fruit water-holding and storage capacity. During the storage of apple and grape fruits, H_2S fumigation could reduce the accumulation of sugars and the content of soluble proteins (Ni et al. 2016; Zheng et al. 2016). However, opposite results were obtained for kiwifruit, strawberry and mulberry fruits (Gao et al. 2013; Hu et al. 2012, 2014a). This may be related to the differences in sugar/acid ratio among different fruit species. Interestingly, H_2S treatment also increased the contents of titratable acid and vitamin C in kiwifruit, grape and mulberry fruit (Gao et al. 2013; Ni et al. 2016; Zhu et al. 2014), which is conducive to the reduction of sugar/acid ratio and prolonging of storage time. In different plant species, H_2S significantly inhibits the respiration rate of fruits and maintains the stability of energy metabolism during postharvest storage. H_2S enhances the activities of H^+-ATPase, Ca^{2+}-ATPase, CCO and SDH in banana pulp, and participates in the regulation of energy metabolism in the fruit (Li et al. 2016a).

H_2S also delays the change in fruit color (Yao et al. 2018), through delaying the degradation of chlorophyll and inhibiting the production of carotenoids, which has been found in both kiwifruit and banana peels (Gao et al. 2013; Ge et al. 2017). In addition, H_2S treatment inhibited the accumulation of anthocyanins (Hu et al. 2014a), which also inhibits the change in fruit color. Meanwhile, H_2S affects the levels of flavonoids and phenols in fruits. The contents of flavonoids and phenols in apple and grape fruits were increased after treatment with NaHS (Ni et al. 2016; Zheng et al. 2016), which would delay fruit senescence and decay. In addition, the metabolism of amino acids in fruits is regulated by H_2S as well. H_2S increases the content of Pro in banana pulp by enhancing the activity of proline synthase P5CS and inhibiting that of SDH (Luo et al. 2015). The metabolism of phenylalanine is affected by H_2S, which can increase the activity of PAL, and thus reduce the content of phenylalanine in fruits (Hu et al. 2014b; Zheng et al. 2016). H_2S also inhibits the activity of PG (Hu et al. 2012) and EGase (Zhang et al. 2014), indicating that H_2S maintains the firmness of fruit by keeping the integrity of cell wall. A recent study showed that endogenous H_2S plays a role in fruit ripening in tomato, for the *SlLCD1* gene-edited mutant displays accelerated fruit ripening (Hu et al. 2020b).

Inhibition of endogenous ethylene synthesis and signal transduction is one of the important mechanisms for H_2S treatment to delay fruit ripening. H_2S treatment could prolong the storage time of "*Red Fuji*" apple, and delay the ripening of apple fruit by suppressing the expression of ethylene synthesis-related genes (*MdACS1*, *MdACS3*, *MdACO1* and *MdACO2*) and signal transduction genes (*MdETR1*, *MdERS1*, *MdERS2*, *MdERF3*, *MdERF4* and *MdERF5*) (Zheng et al. 2016). Similarly, H_2S inhibits the expression of ethylene-related genes (*SlACO1*, *SlACO3*, *SlACO4*; *SlETR5*, *SlETR6*, *SlCRF2*, and *SlERF2*) in tomato (Hu et al. 2019). Compared with the control, H_2S treatment down-regulated the ethylene biosynthesis genes (*MaACS1*, *MaACS2*, *MaACO*1 and pectin lyase *MaPL*), while up-regulated the ethylene receptor genes (*MaETR*, *MaERS1* and *MaERS2*) in banana fruit (Ge et al. 2017).

NO can bind with ACC oxidase to form a stable "ACC-ACC oxidase-NO" ternary complex in a dose-dependent manner (Mukherjee 2019). This signaling event in turn leads to a decrease in ethylene production in tissues. Ethylene accumulation was reduced in peach fruits under treatment with H_2S and NO donors (Zhu et al. 2014). NO-H_2S crosstalk showed a stable synergistic effect to inhibit ethylene-induced fruit ripening. Zhang et al. (2014) reported that the combination of exogenous H_2S and NO could alleviate ROS stress, improve fruit firmness, and enhance the anti-ripening effect of strawberry fruit. Liu et al. (2011) clarified the downstream position of H_2S in the ethylene-NO-H_2S signaling pathway. The signal transduction of H_2S with ethylene during fruit ripening has been reviewed (Ziogas et al. 2018). In these processes, H_2S interacts with ROS and RNS stress signals. The S-persulfidation and S-nitrosylation by H_2S and NO directly occur in plants, which is also an important way for them to regulate plant maturation (Huo et al. 2018; Ziogas et al. 2018).

MULTIPLE CROSSTALK OF H_2S, NO AND H_2O_2 SIGNALS IN PLANTS

Organisms have evolved metabolisms as well as regulatory mechanisms for adaptation to the changing atmospheric composition during Earth's history: from H_2S to NO to O_2, and from ancient to the present (Yamasaki and Cohen 2016). Hence, a great deal of research evidence has shown that the traces of environmental changes left in organisms might marvelously evolve into more complex signal crosstalk and regulatory mechanisms. Either in mammal or plant cells, the special actions, functions and mechanisms of H_2S (RSS), NO (RNS) and H_2O_2 (ROS) are inseparable from their inherent chemical properties and oxidative PTMs. Here, we focus on the clues to help a better understanding of the multiple signals of H_2S, NO and H_2O_2 in plants.

Chemical characteristics and signals: H_2S (RSS), NO (RNS) and H_2O_2 (ROS)

As a gas molecule, H_2S has a classic "V-type" molecular structure, which is similar to the molecular structure of H_2O. Gaseous H_2S has active chemical properties, and is soluble in water (Kimura 2015), forming weak acid known as "hydrogen sulfuric acid". Its aqueous solution contains hydrogen sulfate HS^- (pK_{a1} = 6.9 in a 0.01–0.1 mol/L solution at 18 °C) and S^{2-} (pK_{a2}, between 12 and 17) (Filipovic et al. 2018), as follows:

$$\text{Step 1}: H_2S \rightleftharpoons H^+ + HS^-,\ pK_{a1} = 6.88$$

$$\text{Step 2}: HS^- \rightleftharpoons H^+ + S^{2-},\ pK_{a2} = 12 \sim 17$$

At the beginning, hydrogen sulfuric acid is clear, but becomes turbid after being placed for a period of time. This is because hydrogen sulfuric acid will react slowly with oxygen dissolved in water to produce elemental sulfur insoluble in water:

$$2H_2S + O_2 = 2S\downarrow + 2H_2O$$

In vivo, the concentration of H_2S is low. Hence, inhaling of excessive H_2S will promote the oxidation self-rescue of organisms, and oxidize H_2S into sulfite and sulfate with low toxicity (Baillie et al. 2016). In addition, channeling of the surplus sulfur to the formation of S-metabolites like thiols is a main way to reduce the toxicity in plants (Baillie et al. 2016). Since S ion in H_2S is in the low divalent oxidation state, H_2S only undergoes oxidation as a reducing agent (Koppenol and Bounds 2017). Oxidation leads to the formation of sulfate (SO_4^{2-}), sulfite (SO_3^{2-}), thiosulfate ($S_2O_3^{2-}$), persulfides (RSS^-), organic (RSS_nSR), inorganic (H_2S_n) polysulfides, and elemental sulfur (S_n). Compared with the direct oxidation of H_2S by O_2, which has a strong thermodynamic barrier, ROS is more naturally involved in this process in vivo (Koppenol et al. 2010). The initial oxidation product of H_2S is the sulfuryl free radical ($HS^\bullet$) that can react with electron donors including ascorbate and GSH. Importantly, the one-electron oxidation of H_2S can initiate oxygen-dependent free radical chain reactions to amplify the initial oxidative event (Carballal et al. 2011; Das et al. 1999). The reaction with hydroperoxides (HOOH) initially forms HSOH, which can react with a second HS^- to form HSSH, that is, polysulfide (Carballal et al. 2011; Hoffmann 1977). In the case of H_2O_2, the final products depend on the initial ratio of H_2O_2 to H_2S and mainly consist of polysulfides, elemental sulfur and sulfate in the presence of excess oxidant (Hoffmann 1977). According to the chemical and computational studies, H_2S probably acts as a direct scavenger of oxidants in biological systems. However, compared with that of LMW thiols, the reaction of H_2S with some oxidants displayed relatively high rate constants, and thus, the content of H_2S (sub micromolar) in the tissues is relatively low (Koike et al. 2017). Besides, H_2S cannot compete with thiols to bind one- and two-electron oxidants at such low concentrations (Filipovic et al. 2018). This means that the direct reaction of H_2S with oxidants is not fast enough in the biological environment to support a significant scavenging effect unless sufficient exogenous H_2S is applied, as mentioned in the previous section. In conclusion, the biological "antioxidant" effects of H_2S can be ascribed to the superimposed effect of the direct chemical action of H_2S itself and indirect effects via enzymes, transporters and other companions.

In the active form of $NO^\bullet$, NO participates in many physiological processes in mammals, such as immune defense, vasodilation and neuro-transmission (Bogdan 2001; Palmer et al. 1988; Santos et al. 2015), which are mediated by the coordination of $NO^\bullet$ with the heme iron in sGC, and then the generation of cyclic guanosine monophosphate (cGMP; a classical second messenger) is activated (Friebe and Koesling 2003; Jahshan et al. 2017). H_2S interweaves with NO signaling, either by reacting with $NO^\bullet$ or its downstream regulatory network or by modulating NO production and cGMP levels in vivo (Bucci et al. 2010; Cuevasanta et al. 2015b; Da Silva et al. 2017; Hancock and Whiteman 2015; Zhang et al. 2017). The direct reaction between NO and H_2S was reported more than a century ago, and gaseous NO can react with gaseous H_2S to produce N_2O, polysulfides (H_2S_n) and elemental sulfur (Dunnicliff et al. 1931; LeConte 1847; Miyamoto et al. 2017; Pierce 1929). However, this is obviously not a one-step reaction, and HNO exists as the actual intermediate of the reaction, which has also been verified in vivo (Yong et al. 2011, 2010). Strangely, single electrons are transferred directly from HS^- to $NO^\bullet$ to produce HNO and $S^{\bullet-}$ is thermodynamically unreasonable ($\Delta G\,0' = +102$ kJ/mol) (Koppenol and Bounds 2017). An alternative mechanism is the formation of $HSNO^{\bullet-}$, a powerful reducing agent,

$$NO^\bullet + HS^- \rightarrow HSNO^{\bullet-}$$

which can initiate a cascade of reactions to result in the formation of N_2O, H_2S_n and S_n (Arulsamy et al. 1999; Suarez et al. 2015). Interestingly, as a key node in the chemical reaction between NO and H_2S, HSNO was also found in the reaction pathways of H_2S with "NO^+" carriers: acidified nitrite, N_2O_3, metal nitrosyls, and S-nitrosothiols (Filipovic et al. 2012; Nava et al. 2016). Among them, N_2O_3 reacts with H_2S to produce HSNO, which may be important for intracellular RSNO generation:

$$N_2O_3 + H_2S \rightarrow HSNO + HNO_2$$

This reaction was detected to occur in the lipid bilayer of the cell membrane where a large amount of N_2O_3 is generated by accumulated NO and O_2, which then reacts with the same large amount of H_2S (Cuevasanta et al. 2012; Lancaster 2017) (Fig. 3). In the reaction of HSNO and thiols, HSNO acts as an "NO^+" carrier that mediates transnitrosation between proteins and across the cell membrane. In addition, the reaction of RSNO and H_2S promotes the extracellular formation of HSNO, but on the contrary, HSNO reacts with RSH to release RSNO and H_2S once entering the cell (Filipovic et al. 2018), which is also considered as an efficient way for H_2S to penetrate the cell membrane (Fig. 3). These findings seem to reveal the profound mechanism of the complementary relationship between NO and H_2S in plant physiology. Since the chemical interaction occurring between NO and H_2S can produce H_2S_n, an enhanced version of H_2S signal in mammals (Kimura

et al. 2015; Miyamoto et al. 2017), it should be determined whether H_2S_n exists or has special physiological effects in plants.

Pivotal post-translational modifications: persulfidation, S-nitrosylation and S-sulfenylation

Recent studies have revealed that the persulfidation of protein cysteine residues (RSSH) acts as an important mechanism of H_2S signaling in plants. Since the protein PTMs mediated by H_2S, NO and ROS occur all by attacking the cysteine residues, we will discuss the persulfidation, S-nitrosylation and S-sulfenylation together in this section.

Protein persulfidation (alternatively called S-sulfhydration) has been identified to be involved in the sulfide-signaling pathway, in which the cysteine thiol (RSH) is persulfidated into a persulfide thiol (RSSH) (Fig. 4). Afterwards, this post-modification may cause functional changes in activities, structures, and subcellular localizations of the target proteins (Aroca et al. 2018). In mammals, persulfidation has been proven to be present on cysteine residues of various proteins, such as K_{ATP} channels (Mustafa et al. 2011), TRP channels (Liu et al. 2014), Kelch-like ECH-associated protein 1 (Keap-1) (Hybertson et al. 2011; Wakabayashi et al. 2004; Yang et al. 2013), p66Shc (Xie et al. 2014b), receptor for AGE (RAGE) (Ramasamy et al. 2011; Zhou et al. 2017), Parkin (an E3 ubiquitin ligase) (Vandiver et al. 2013), Nuclear factor κB (NF-κB) (Du et al. 2014; Sen et al. 2012) and Glyceraldehyde Phosphate Dehydrogenase (GAPDH) (Gao et al. 2015; Mustafa et al. 2009). Interestingly, the series of studies of Kimura's team have revealed that H_2S_n can also mediate similar PTMs as H_2S in mammalian cells, and is more effective than NaHS (Kimura 2015; Kimura et al. 2015). The occurrence of persulfidation mediates the 3-dimensional conformation of the corresponding proteins by changing the properties of cysteine residues and the disulfide bonds, thus, affecting the activity and function of proteins.

In recent years, there has been certain progress in the research on persulfidation in plants due to the advanced detection methods and the corresponding omics analysis. Previously, the biotin switch method (BSM) was widely used for the detection of PTMs by S-nitrosylation (Sell et al. 2008). After three steps of blocking by thiol-blocking reagent methyl methanethiosulfonate (MMTS), reducing by ascorbate and connecting with *N*-6-(biotinamido) hexyl-3′-(2′-pyridyldithio)-propionamide (biotin-HPDP) to form biotin-labeled proteins, RSNO could finally form biotin-labeled proteins (Mustafa et al. 2009). Aroca et al. (2015) detected a total of 106 persulfidated proteins through the modified BSM. Subsequently, they developed a comparative and quantitative proteomic analysis approach for the detection of endogenous persulfidated proteins in Col-0 and *des1* mutant leaves using the tag-switch method. They identified 2330 potential target proteins for persulfidation (Aroca et al. 2017, 2018). KEGG and GO analysis showed

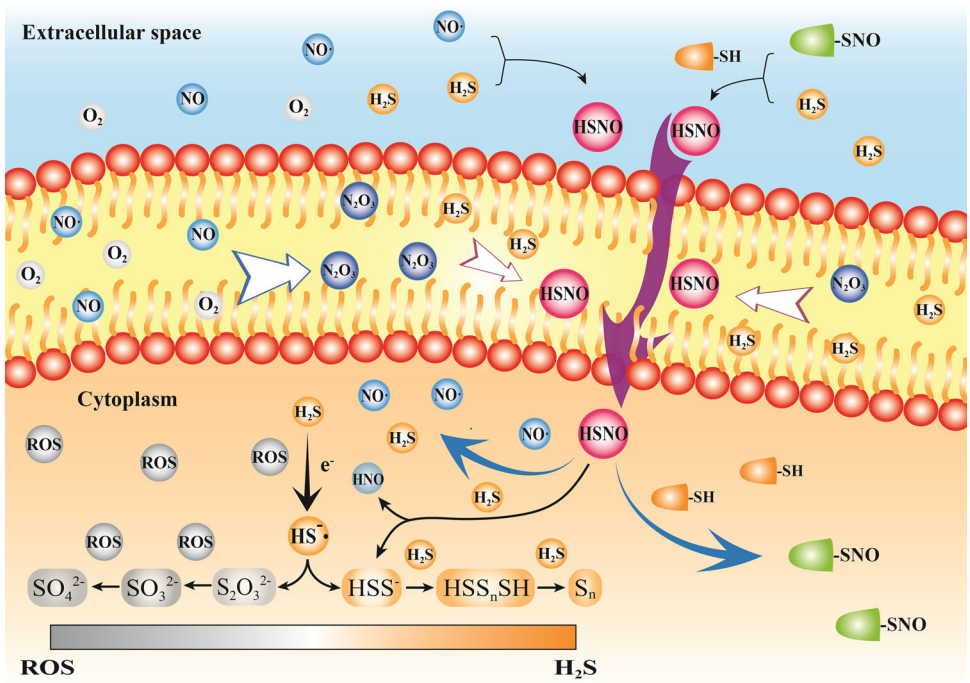


Fig. 3 Endogenous chemical signals in plants involving H_2S, NO and ROS. N_2O_3 is synthesized by NO and O_2 accumulated in the bilayer of cell membrane, and then forms HSNO with H_2S. Extracellularly, HSNO can be directly synthesized by H_2S and NO. HSNO can enhance the membrane permeability of H_2S and NO, which is also the transmembrane transfer mode of cysteine thiols. Intracellularly, H_2S undergoes oxidation and generates sulfate (SO_4^{2-}), sulfite (SO_3^{2-}), thiosulfate ($S_2O_3^{2-}$), persulfides (RSS^-), organic (RSS_nSR), inorganic (H_2S_n) polysulfides, and elemental sulfur (S_n), which is controlled by different ratios of H_2S and ROS level

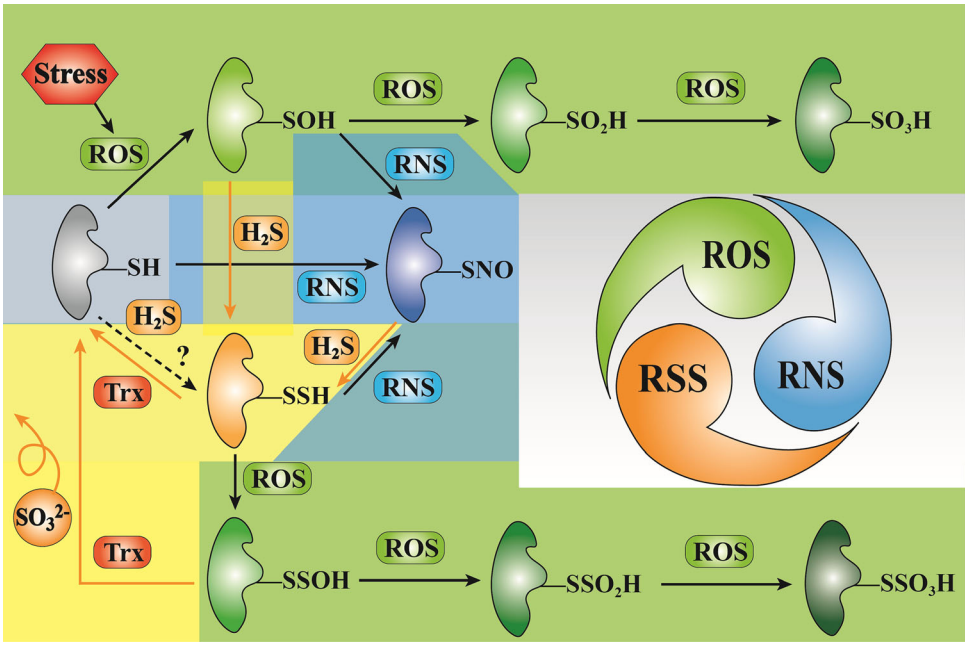


Fig. 4 Multiple post-translational modifications on cysteine residues of proteins. Protein cysteine thiols (RSH) can be sulfonated to produce RSOH with increasing ROS. Upon continuous exposure to ROS, RSOH could further generate irreversible sulfinic (RSO_2H) and sulfonic acids (RSO_3H). On the basis of RSOH, H_2S and NO can be persulfidated and S-nitrosylated, respectively, to produce RSSH and RSNO. In the presence of nitrotransferase, NO can also react directly with RSH to produce RSNO. Once persulfidated cysteine thiols encounter ROS, RSSH will rapidly react with ROS to form adducts (RSSOH, $RSSO_2H$ and $RSSO_3H$). Among them, RSSH and RSSOH can be reduced back to thiols by the action of the thioredoxin (Trx)

that the proteins possibly regulated by persulfidation mainly exist in the cytoplasm and chloroplast, and are involved in processes such as carbon metabolism, abiotic and biotic stress responses, plant growth and development, and RNA translation (Aroca et al. 2017). A differential analysis of the persulfidated proteins of *des1* and Col-0 highlighted the importance of H_2S produced by DES1, which initiates persulfidation and regulates downstream signals. As expected, DES1-generated H_2S-induced S-persulfidation, which was involved in the regulation of stomatal movement in *Arabidopsis*. In the process of stomatal response to ABA induction, DES1 can self-persulfidate under the action of H_2S at Cys44 and Cys205, which is important for the amplification of H_2S signal (Shen et al. 2020). Moreover, sustainable H_2S accumulation could drive the persulfidation of the NADPH oxidase RBOHD at Cys825 and Cys890, enhancing its ability to produce ROS (Shen et al. 2020). Similarly, SnRK2.6/OST1 has been identified to be persulfidated at Cys131 and Cys137, which activates the kinase during ABA-induced stomatal closure (Chen et al. 2020). It is worth mentioning that Cys137 can also be modified by S-nitrosylation, while the difference is that the NO-mediated PTM inhibits the kinase activity (Wang et al. 2015). All these findings reveal the importance and infinite possibility of cysteine thiol modification, especially sulfhydryl modification, in stomatal movement of plants. In addition, H_2S-mediated persulfidation has also been found to regulate other plant signaling pathways. The occurrence of persulfidation induced by H_2S can specifically activate cytosolic CAT, APX and GAPDH in cytoplasm (Aroca et al. 2015; Palma et al. 2020), which is also the classic enzyme-dependent pathway of ROS scavenging by H_2S. In addition, H_2S negatively controls the progress of autophagy through specifically persulfidating Cys170 residue of the ATG4a protease in *Arabidopsis* (Laureano-Marín et al. 2020). Then, the post-translational processing of ATG8 and the synthesis of autophagosomes are prevented (Laureano-Marín et al. 2020). In addition to positive regulation of ROS scavenging, H_2S-mediated persulfidation also has some negative effects. Excessive accumulation of H_2S reduces the density of F-actin bundles and the F-actin/globular actin ratio, because persulfidation occurs at the Cys293 residue of ACTIN2, which prevents actin polymerization and then inhibits the development of root hair in *Arabidopsis* (Aroca et al. 2017; Li et al. 2018a). This coincides with studies in animals. H_2S not only dynamically regulates the depolymerization of actin, but also affects the stability of tubulins in mammals (Mustafa et al. 2009). In tomato, H_2S treatment could persulfidate the ACC oxidases LeACO1 and LeACO2, and inhibit their activities (Jia et al. 2018a), suggesting that ethylene-induced H_2S negatively regulates ethylene biosynthesis

by persulfidation of LeACOs. In general, the physiological functions of H_2S in plants are far more than we mentioned above, and the biological significance of the persulfidation of protein cysteine mediated by H_2S is worth of further exploration.

S-nitrosylation, an NO-mediated protein PTM, is another type of cysteine thiol modification. The concept of S-nitrosylation was first proposed in 1994, meaning that exposure to high concentrations of NO promotes protein cysteine residue thiols (RSH) to form RSNO, which regulates the signal transduction of redox (Stamler 1994) (Fig. 4). RSNO is relatively stable, and is therefore considered as the major form for the storage and transport of NO, but it is sensitive to strong reducing agents (i.e., intracellular GSH and ascorbate), and extremely sensitive to metal ions, especially Fe^{2+} and Cu^{2+} (Hogg 2002). Moreover, RSNO can further react with thiols to produce disulfide (RSSR) and HNO (Wong et al. 1998). When reacting with H_2S, the product is HSNO. However, an alternative reaction is the formation of HNO and a protein persulfide (RSSH), which is thermodynamically unfavored (Koppenol and Bounds 2017), whereas some protein microenvironments could facilitate this reaction. Different from the similar function of H_2S and NO, persulfidation and S-nitrosylation might regulate protein functions differentially. In an omics study of mammals, the persulfide and S-nitrosothiol proteomes were reported to have a 36% overlap (Gao et al. 2015). In plants, the relationship between S-nitrosylation and persulfidation has been gradually revealed (Fig. 4). NO and H_2S have a synergistic relationship in many pathways, which can not only promote each other's enzyme activity, but also relieve the effects of various stresses. Surprisingly, relative to S-nitrosylation, persulfidation showed opposite effects on SnRK2.6/OST1 (Wang et al. 2015), actins (Rodriguez-Serrano et al. 2014), APX1 (Begara-Morales et al. 2014) and GAPDH (Vescovi et al. 2013). S-Nitrosylation and persulfidation regulate cysteine thiols at the same site (GAPDH at adjacent locus), but have the opposite effect (inhibiting or promoting) on their activities. In *Arabidopsis*, a total of 623 candidate proteins were identified to be S-nitrosylated and persulfidated (Aroca et al. 2018), which greatly expands the scope of research on the modification of cysteine thiols.

When exposed to ROS, protein cysteine thiols can be oxidized to sulfenic acid (RSOH), that is S-sulfenylation. Then, RSOH could be further oxidized with the formation of irreversible sulfinic (RSO_2H) and sulfonic acids (RSO_3H) (Filipovic and Jovanovic 2017) (Fig. 4). Moreover, H_2S could react with sulfenic acid to form persulfides (RSSH), and this process is termed as persulfidation. After the completion of persulfidation, RSSH has bidirectional redox ability, and can be reduced back to thiols under the action of thioredoxin (Trx), or rapidly react with ROS/RNS to form an adduct ($RSSO_3H$) under exposure to ROS. The $RSSO_3H$ also could be cleaved by Trx to restore free thiol and by-product sulfite (Filipovic and Jovanovic 2017; Wedmann et al. 2016) (Fig. 4). Under the dynamic action of ROS and Trx, RSH and RSSH jointly construct the endogenous cycle of H_2S (Wedmann et al. 2016), that is, H_2S is recycled and reused by the cells. The formation of $RSSO_3H$ is also an adaptive short-term storage method to alleviate the surge of endogenous ROS and RNS in plants. Notably, there is still no solid evidence that H_2S acts directly on cysteine thiols during the occurrence of persulfidation (Cuevasanta et al. 2015a), such as the discovery of related catalytic enzymes. Hence, RSOH is considered as an important intermediate for S-sulfenylation, persulfidation and even S-nitrosylation. Besides, H_2S_n could be another potential way of H_2S-induced persulfidation, which is produced by the oxidation of H_2S or by enzymes such as 3-MST to directly S-sulfurate cysteine residues (Kimura et al. 2013, 2015). In mammals, previous studies have revealed that these three oxidative modifications of proteinaceous cysteinyl thiols can be converted to each other, when one of the evoked signals is dominant (Hancock and Whiteman 2016a, b), corresponding modification is more likely to occur on the key cysteine site. These findings show that the modification mode induced by H_2S, NO and H_2O_2 is strongly dose dependent, which may explain why the downstream signal response is much more intense when exogenous donors are used. Intriguingly, without the interference of dose effect, these three kinds of oxidative modifications also have discrepancies in oxidation ability, following the order of S-persulfidation (RSSH) > S-nitrosylation (RSNO) > S-sulfenylation (RSOH) (Hancock and Whiteman 2016a; Olson 2015; Wang 2012), which not only illustrates the mediating role of oxidized cysteine thiols, but also highlights the priority of S-persulfidation in the competition for modifying cysteine residues. Accordingly, it seems that these three kinds of modifications based on cysteine thiols are mutually regulated and transformed. For the mammalian MST, a stable persulfide at cysteine Cys247 can be oxidized by H_2O_2 to form Cys-thiosulfenate, Cys-thiosulfinate, and Cys-thiosulfonate, and then Trx can convert these modified cysteines to nonmodified cysteines (Nagahara et al. 2012). Recently, a total of 1,537 S-sulfenylated sites on more than 1000 proteins were identified in *Arabidopsis*. Compared with human S-sulfenylation datasets, 155 conserved S-sulfenylated cysteines were provided, including Cys181 of the *Arabidopsis* MAPK4 (Huang et al. 2019). RSOH is not only

the specific protein regulated by sulfenylation of cysteine thiols, but also the basis of dynamic regulation of the three modifications. Moreover, comparisons across different databases will help to identify the target proteins regulated by the triple regulations.

PERSPECTIVES

The impact of gasotransmitter H_2S on vegetation is paradoxical, as excessive H_2S negatively affects plant growth and development, while plants can utilize low levels of H_2S as a dynamic regulator for survival (Ausma and De Kok 2019). H_2S can effectively delay the flowering process of plants (Zhang et al. 2011), which is considered as a secondary regulatory pathway to inhibit the PCD process (Romero et al. 2014). However, several recent reports have suggested that H_2S is involved in the regulation of plant flowering by transcriptional regulation and PTMs. The more specific mechanism by which H_2S affects flowering deserves further exploration.

Many kinds of stress stimuli and growth signals can induce the production of endogenous H_2S through enzymatic pathways. For example, exogenous H_2S activates DES1 through persulfidation (Chen et al. 2020), and *TGA3* promotes the increase in *LCD* transcription level (Fang et al. 2017). However, little is still known about the regulation mode of the H_2S-producing enzymes, which is also worth of more studies.

H_2S-induced persulfidation has been proved to be an important PTM in animals and plants. Among all the modified target proteins, ion transporters are undoubtedly an important class. In mammals, various types of ion channels (K^+_{ATP} channels, K_{Ca} channels, Ca^{2+} channels, Cl^- channels and TPR channels) have been confirmed to be modified and regulated by H_2S-induced persulfidation (Lefer 2019; Wang 2012; Yang et al. 2019). In plants, exogenous H_2S can inhibit the transport of inward-rectifying K^+ channels (I_{KIN}) (Papanatsiou et al. 2015) and activate SLAC1 currents (Wang et al. 2016) in plant guard cells, but it remains unclear whether there is a direct persulfidation process. A large amount of omics data in plants also indicate the potential regulatory effect of persulfidation on the activity of ion channels (Aroca et al. 2017, 2018; Wedmann et al. 2016), but there is still a lack of more intuitive experimental evidence.

Lastly, due to the complexity of the dynamic changes of ROS, RNS and RSS, it is difficult to predict the modification mode of protein cysteine residues. Although many progresses and conjectures have been made in biochemical studies, there are still no strong evidence and clear understanding on the property of RSH at the molecular level, such as whether the node effect of RSOH is universal, whether H_2S forms RSSH directly by the enzymatic way, the dose effect, and competition relationship between RSNO and RSSH. These are undoubtedly challenging research direction in the future.

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Compliance with ethical standards

Conflict of interest All the authors state that there is no conflict of interest.

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