



Review

Hydrogen Sulfide in Plants: Crosstalk with Other Signal Molecules in Response to Abiotic Stresses

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Abstract: Hydrogen sulfide (H₂S) has recently been considered as a crucial gaseous transmitter occupying extensive roles in physiological and biochemical processes throughout the life of plant species. Furthermore, plenty of achievements have been announced regarding H₂S working in combination with other signal molecules to mitigate environmental damage, such as nitric oxide (NO), abscisic acid (ABA), calcium ion (Ca²⁺), hydrogen peroxide (H₂O₂), salicylic acid (SA), ethylene (ETH), jasmonic acid (JA), proline (Pro), and melatonin (MT). This review summarizes the current knowledge within the mechanism of H₂S and the above signal compounds in response to abiotic stresses in plants, including maintaining cellular redox homeostasis, exchanging metal ion transport, regulating stomatal aperture, and altering gene expression and enzyme activities. The potential relationship between H₂S and other signal transmitters is also proposed and discussed.

Keywords: hydrogen sulfide; nitric oxide; abscisic acid; Ca²⁺; hydrogen peroxide; abiotic stresses; signal transmitters; stomatal movement



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1. Introduction

Several abiotic stresses such as salt, drought, flooding, heat, cold, and freezing easily result in the loss of crop production and a drop in economy in the world. Furthermore, with ongoing industrialization and pesticides application, plants are more likely subjected to some abiotic stresses including salinity and heavy metal (aluminum (Al); cadmium (Cd); chromium (Cr); lead (Pb); cobalt (Co); arsenic (As); nickel (Ni)) stresses [1,2]. In order to survive, plants must make a series of adjustments in morphology and physiological and biochemical metabolism when they are subjected to abiotic stresses. There are many kinds of mechanisms for plants to respond to abiotic stresses, including plant hormones, osmotic regulators, active oxygen scavenging systems, genes, and proteins. When plants are subjected to adversity stress, a series of changes will occur in the hormone levels, thereby initiating or regulating certain physiological and biochemical processes related to stress resistance to complete the response to adversity. Moreover, some inorganic and organic osmotic substances such as Na⁺, K⁺, Cl⁻, proline (Pro), and soluble sugars may accumulate when plants encounter stresses. Further, under normal circumstances, the reactive oxygen species (ROS) are tightly controlled in plants, because plants have a reactive oxygen scavenging system, which keeps the production and removal of reactive oxygen species in a dynamic balance. This ROS includes hydrogen peroxide (H₂O₂), superoxide anion (O₂⁻), singlet oxygen (¹O₂), and hydroxyl radical ([•]OH) [3]. Under the condition of adversity, this balance is broken, and a large amount of active oxygen is produced. Active oxygen attacks the membrane system, causing changes in membrane lipid components and conformation of various enzymes on the membrane, loss of membrane selective permeability, leakage of electrolytes and certain small molecular organic substances, and disorder of mitochondria and chloroplast functions [1,4]. The active oxygen scavenging system mainly includes two types of substances: one is an enzymatic protection system composed of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT), etc.; the

other is non-enzymatic antioxidants including reduced glutathione (GSH), carotenoids (Car), vitamin E, and other antioxidants [5]. Last but not least, some proteins such as NAC, WRKY, basic region/leucine zipper motif (bZTP), and salt overly sensitive1 (SOS1) participate in plant response to abiotic stresses [2,6].

Hydrogen sulfide (H_2S) is a colorless, combustible, and hydrosoluble gas with an obvious smell of rotten eggs, which has been widely considered as the third gasotransmitter molecule besides nitric oxide (NO) and carbon monoxide (CO) [7]. The emission of H_2S was studied a long time ago. In 1978, Wilson et al. (1978) firstly observed the emission of H_2S in the leaves of cucumber (*Cucumis sativus* L.), squash and pumpkin (*Cucurbita pepo* L.), cantaloupe (*Cucumis melo* L.), maize, soybean (*Glycine max* L. Merr), and cotton (*Gossypium hirsutum* L.) [8]. Current studies show that H_2S can be biosynthesized through a variety of enzymes such as cysteine synthase (CS), β -cyanoalanine synthase (CAS), L-cysteine desulfhydrase (LCD), D-cysteine desulfhydrase (DCD), and sulfite reductase (SiR) in mitochondria, cytosol, and chloroplast [9,10]. In mitochondria, H_2S can be produced by CAS in the course of cyanide detoxification. The generation of H_2S mainly occurs by inducing the activities of LCD and DCD from cysteine (Cys) in the cytosol, which is also accompanied by the formation of pyruvate and ammonia. SiR is the reaction catalyst in the photosynthetic sulfate-assimilation pathway which induces the release of H_2S in the chloroplast [11,12]. Thus, endogenous H_2S can be produced under the catalysis of the corresponding enzymes [8–11]. The changes in endogenous H_2S level can influence cellular metabolisms, enzyme activities, and gene expressions, and thus modulate plant growth and development [5,13]. Therefore, H_2S is widely considered as a signaling molecule within organic cells.

In the last few decades, increasing evidence has shown that H_2S plays a vital role in the treatment of diseases for animals and humans, including cancer [13], burns [14], neurodegenerative diseases [15], and inflammation [16]. In addition, it is involved in many processes of growth and development in plants. It can influence the seed germination, root organogenesis, photosynthesis, stomatal movement, leaf senescence, fruit ripening and nodulation, and nitrogen fixation [17]. H_2S can also enhance the plant's tolerance to diverse biotic and abiotic stresses, such as bacterial and fungal pathogens, salinity, drought, heat, hyperosmotic, oxidative and heavy metal stresses, etc. [5,17–19].

As a gaseous signaling molecule, H_2S can interact with other signal molecules to influence the growth and development of, and respond to abiotic stresses in, plants. Plenty of research demonstrates that H_2S is involved in NO-alleviated salt stress and heavy metal stresses in the seedling roots of pea (*Pisum sativum* L. cv. Azad P-1) and barley (*Hordeum vulgare* L.), as well as the seeds of alfalfa (*Medicago sativa* L. cv. Victoria) [20–22]. Besides, some plant hormones such as abscisic acid (ABA), salicylic acid (SA), ethylene (ETH), jasmonic acid (JA), and melatonin (MT) could alleviate abiotic stresses together with H_2S in the process of plant growth and development. Some ionic signals such as calcium ion (Ca^{2+}) and H_2S are interrelated under stresses [23]. Meanwhile, H_2O_2 and proline (Pro) have been reported to have a relationship with H_2S under abiotic stresses during the process of plant growth [17,24,25]. Here, we comprehensively review the crosstalk between H_2S and other signal molecules in response to abiotic stresses. Also, new research directions and future prospects in this area will be discussed in this review (Figure 1).

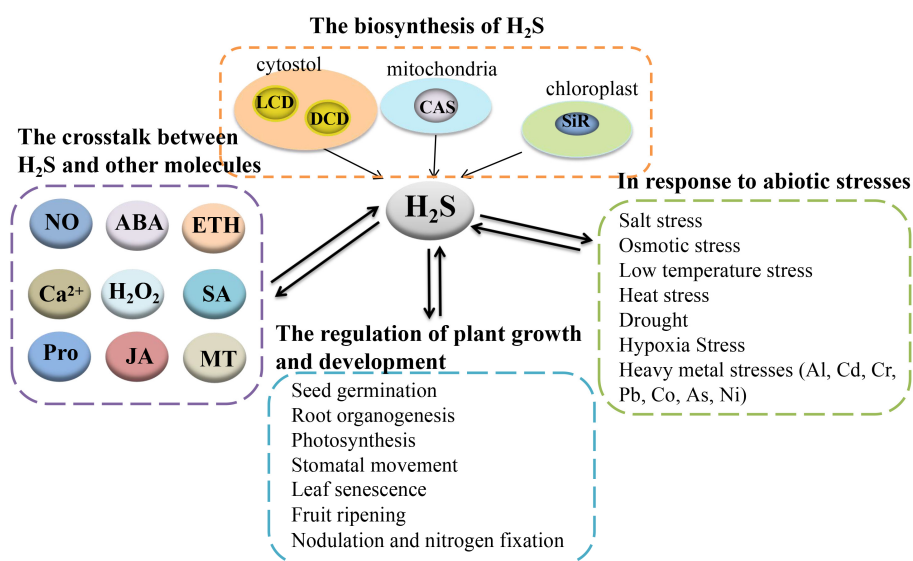


Figure 1. The summary of the biosynthesis of H_2S , the crosstalk between H_2S and other molecules, the regulation of plant growth and development, and the response to abiotic stresses by H_2S . H_2S , hydrogen sulfide; LCD, L-cysteine desulphydrase; DCD, D-cysteine desulphydrase; CAS, β -cyanoalanine synthase; SiR, sulfite reductase; NO, nitric oxide; ABA, abscisic acid; Ca^{2+} , calcium ion; H_2O_2 , hydrogen peroxide; SA, salicylic acid; JA, jasmonic acid; Pro, proline; MT, melatonin; Al, aluminum; Cd, cadmium; Cr, chromium; Pb, lead; Co, cobalt; As, arsenic; Ni, nickel.

2. Crosstalk between H_2S and NO in Response to Abiotic Stresses

NO is widely recognized as a gas transmitter in the regulation of seed germination, dormancy, stomatal aperture, adventitious root development, and photosynthesis in plants [26,27]. NO also takes part in many stress alleviation processes, such as heavy metal, extreme temperature, drought, salt, and UV-B radiation [4,28]. Moreover, the relationship between H_2S and NO under different stress conditions has been explored at both the physiological and molecular levels, which remains a hot topic in plant science research in recently years. The obtained achievements in this field were collected and shown below.

2.1. Crosstalk between H_2S and NO in Response to Heavy Metal Stress

There is considerable research on how H_2S and NO interplay with each other in plants under heavy metal stress. In pea seedlings, As (V) reduced growth, photosynthesis capacity, and nitrogen content [29]. An application of exogenous NaHS alleviated As (V) toxicity by inducing H_2S and NO generation. These results suggest a vital role of H_2S in As (V) stress tolerance. Also, exogenous H_2S and NO could reduce the influence of Cr (VI) toxicity in maize (*Zea mays* L.) in a similar manner [30]. Furthermore, H_2S donor NaHS and NO donor sodium nitroprusside (SNP), rather than other derivatives, were found to specifically ameliorate Cd-induced oxidative damage in the root tissues of alfalfa seedlings [31]. This work further confirms that both H_2S and NO may participate in alleviating heavy metal stress. In addition, the alleviation effects of NaHS and SNP were reversed by NO scavenger 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazole-1-oxyl-3-oxide potassium salt (cPTIO) [31], illustrating crosstalk between H_2S and NO during the response to Cd stress. Another study in wheat (*Triticum aestivum* L.) obtained similar results that exogenous H_2S might correlate with NO to enhance Co tolerance [32]. The above studies show that H_2S may cooperate with the NO signal in managing different heavy metal stresses in plants.

The pharmacological method of introducing specific scavengers into different experimental conditions was further employed to research the relationship between H_2S and NO under heavy metal ion stress in plants. Cd stress was shown to induce a burst of endogenous NO and H_2S in bermudagrass [*Cynodon dactylon* (L). Pers.] [33]. Moreover,

exogenous NO donor SNP and H₂S donor NaHS could improve Cd stress tolerance, while the positive roles of SNP and NaHS were specifically blocked by H₂S scavenger hypotaurine (HT, C₂H₇NO₂S), but not by NO scavenger cPTIO and H₂S inhibitors potassium pyruvate (PP, C₃H₃KO₃) and hydroxylamine (HA, H₃NO). PP is regarded as the substrate of dehydrogenase. H₂S could interact with the dehydrogenase. HA is an alkaline inorganic amine, which can react with the acid gas H₂S; thereby, PP and HA are able to inhibit the production of endogenous H₂S [33]. Thus, NO could activate the H₂S signal in response to Cd stress, and maybe H₂S is downstream of the NO signal. This phenomenon was further proved by the study of Al stress in soybean roots, in which NO modulated *GmMATE13* and *GmMATE47* gene expressions to enhance citrate secretion, and regulated PM H⁺-ATPase activity through regulating H₂S biosynthesis and degradation [34]. H₂S and NO improved Pb tolerance in *Sesamum indicum*, while the H₂S-induced response was completely eliminated by NO scavenger cPTIO [35]. Meanwhile, only part of the effect conducted by NO was weakened by H₂S scavenger HT. It seems that NO acts downstream of H₂S or independent of H₂S in conferring plant tolerance to Pd stress. More recently, the downstream role of NO in cooperation with H₂S was also discovered in pepper (*Capsicum annuum* L.) and wheat under Cd stress [36,37]. From the numerous studies of H₂S and NO, a hypothesis may be drawn that there exists a two-side signal cascades mechanism between H₂S and NO in mediating heavy metal damage (Figure 2).

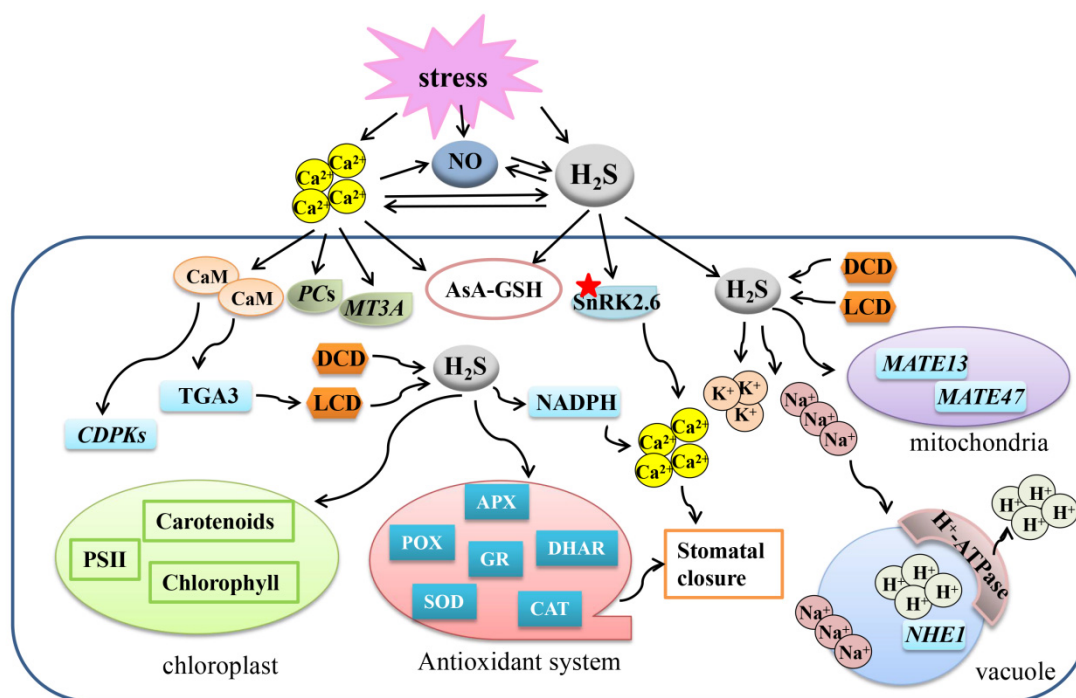


Figure 2. Overview for the mechanisms of the crosstalk between Ca²⁺, NO, and H₂S to regulate plant response to abiotic stresses. A protein marked with a red asterisk means that the protein can be persulfided. Ca²⁺, calcium ion; NO, nitric oxide; H₂S, hydrogen sulfide; LCD, L-cysteine desulphydrase; DCD, D-cysteine desulphydrase; APX, ascorbate peroxidase; SOD, superoxide dismutase; GR, glutathione reductase; POD, peroxidase; CAT, catalase; CaM, calmodulin; PCs, phytochelatin synthase; MT3A, metallothionein-like type 3; CDPKs, Ca²⁺-dependent protein kinases; AsA-GSH, ascorbate-glutathione cycle; DHAR, dehydroascorbate reductase; POD, peroxidase; CAT, catalase.

2.2. Crosstalk between H₂S and NO in Response to Salt Stress

It has long been recognized that H₂S and NO participate in alleviating salt stress in different plant species. Salt treatment (conducted by NaCl) could increase endogenous H₂S and NO generation in the leaves of *Nicotiana tabacum* L. cv. Havana by increasing L-Cys and L-Arg contents and enhancing H₂S and NO biosynthesis enzyme activities [38].

Then, H₂S and NO help plants to cope with oxidative stress induced by salinity. These results suggest that both H₂S and NO contribute to enhancing salt tolerance. Moreover, H₂S donor NaHS and NO donor SNP relieved the inhibition of seed germination under salt stress in alfalfa through reestablishing ion homeostasis and maintaining activities of antioxidant enzymes [39]. The attenuation effect of salinity damage by H₂S was reversed by NO scavenger cPTIO, suggesting that H₂S enhanced salt tolerance through the NO pathway [39]. Another report discovered a similar relationship between H₂S and NO in rescuing salt-induced inhibition of plant growth by regulating ion homeostasis [22].

The relationship between H₂S and NO in salt resistance is still puzzled. It has been found that NO accumulation occurred ahead of H₂S, however, H₂S could not stimulate NO accumulation during the initial stage in salt-treated tomato (*Solanum lycopersicum*) roots [40]. The results above illustrate that H₂S acts downstream of NO under salt stress, and may further induce NO production to strengthen the signal cascade in a feedback manner (Figure 2). In addition, H₂S and NO may act downstream of MT to alleviate salt stress in pepper seedlings [41].

2.3. Crosstalk between H₂S and NO in Response to Other Stresses

There also exists multiple pieces of evidence that H₂S and NO cooperate with each other in heat, drought, osmotic, and flooding stresses. The pretreatment of exogenous NO enhanced the survival rate of maize seedlings under heat stress, and NO increased H₂S content [42]. Furthermore, NO-induced heat tolerance was eliminated by H₂S synthesis inhibitors and a H₂S scavenger [42], indicating that H₂S may act downstream of the NO signal in NO-induced heat tolerance. Later, another study discovered that SNP treatment facilitated the survival of submerged maize by enhancing the antioxidant system and regulating ROS content, elevating intracellular Ca²⁺ content and ADH activity, and increasing expressions of hypoxia-induced genes in maize seedling roots [43]. Moreover, SNP induced endogenous H₂S generation, and H₂S increased the NO-enhanced acquisition of tolerance to flooding-induced hypoxia in maize seedling roots [43], suggesting an analogical pattern of H₂S and NO signal cascades in relieving heat and hypoxia stresses.

H₂S may act as a downstream component of NO in ethylene-induced stomatal closure in *Vicia faba* L. [44]. Also, NO represented downstream of H₂S in ABA-triggered stomatal closure, which may suggest a paradoxical relationship between H₂S and NO under drought condition [45]. As for osmotic stress in wheat seedlings, the application of exogenous NO markedly improved H₂S synthesis enzymes LCD and DCD, as well as enhancing the activity of *O*-acetylserine (thiol)lyase (OAS-TL) to modulate Cys homeostasis [46]. On the other hand, NO scavenger cPTIO and H₂S scavenger HT invalidated the effect of NO on endogenous H₂S levels and Cys homeostasis in wheat [46]. Thus, both H₂S and NO could contribute to reinforcing osmotic tolerance and direct stomatal closure, though the concrete mechanism is largely unknown.

The H₂S donor GYY4137 released a less severe H₂S shock and a more prolonged H₂S flux; however, it decreased NO accumulation in guard cells of *A. thaliana* leaves, in accordance with another type of H₂S donor, NaHS [47]. In *Medicago sativa*, pretreatment with NOSH or NOSH-aspirin, the novel donors, which can donate NO and H₂S simultaneously to plants, could enhance plant tolerance to drought stress and improve the recovery phenotype followed by rewatering [48]. Considering the cooperative relationship between H₂S and NO, acting as signal molecules in retarding environmental damages, NOSH or NOSH-aspirin seems to be more favorable compared with NaHS and GYY4137 when used in plant guard cells, however, the effect and dosage have yet to be demonstrated (Figure 2).

3. Crosstalk between H₂S and ABA in Response to Abiotic Stresses

ABA has long been recognized as a significant phytohormone with the function of regulating plant growth, development processes, and responses to diverse environmental stresses [49]. Within drought stress, ABA may take a central role in endogenous physiological processes, including stomatal movement [50,51]. Stomata are pores of plant aerial

tissues and consist of a pair of guard cells. The stomatal aperture can be modulated by these specialized cells to respond to external and internal stimuli [52]. Within the past 10 years, the research of H₂S and ABA crosstalk in augmenting plant tolerance to abiotic stresses has always come along with the regulation mechanism of stomatal movement.

3.1. Crosstalk between H₂S and ABA in Response to Abiotic Stresses through Regulating Stomatal Closure

H₂S cooperates with ABA in modulating the stomatal aperture, which has long been reported since [53] found that exogenous H₂S regulated stomatal movement and enhanced leaf relative water content (RWC) to strengthen plant drought tolerance in *Arabidopsis thaliana*. Furthermore, scavenging H₂S by HT or inhibiting H₂S biosynthesis partially blocked ABA-dependent stomatal closure through regulating ATP-binding cassette transporters [53]. Similarly, pretreatment with H₂S could considerably enhance rice's tolerance to drought stress by decreasing lipid peroxidation, maintaining antioxidant system activation, and improving ABA biosynthesis [54]. The results above affirm a role of H₂S in ABA signaling under environmental stresses. Furthermore, the stomatal aperture was enlarged in *lcd* mutant plants, causing a sensitive drought phenotype [55]. In addition, *LCD* expression and H₂S generation were down-regulated in ABA-related mutants *aba3* and *abi1*, and NaHS application increased stomatal closure in these mutants [55]. Thus, H₂S may regulate stomatal aperture in an ABA-dependent manner, and ABA may induce H₂S biosynthesis under drought stress. Simultaneously, another report revealed that pretreatment of exogenous H₂S enhanced wheat seedling tolerance to drought conditions through reinforcing antioxidant capacity [56]. Besides, the application of H₂S modulated ABA metabolic pathway genes and up-regulated ABA receptors, indicating again that H₂S alleviates drought stress, at least in part, through the ABA signaling pathway. Furthermore, exogenous ABA induced the endogenous H₂S content under drought stress [56], illustrating a complex relationship between H₂S and ABA signals in modulating drought stress.

Mitogen-activated protein kinases (MAPKs) belong to a crucial signaling molecule family which adjusts plants to multiple environmental stimuli [49]. In *A. thaliana*, drought stress fortified H₂S generation and gene expression of MAPK, however, the induced MAPK expression was abolished in H₂S synthesis double mutants *lcd des1* [57]. Further, the contributions of ABA to stomatal movements were also inhibited in *lcd des1* and *mpk4* mutants. In addition, H₂S-enhanced stomatal closure was impaired in *slac1-3* mutants [57], in which SLAC1 is an S-type anion channel that responds to ABA signaling in stomatal closure [58]. A previous report announced that H₂S could activate S-type anion currents via SLAC1 to induce stomatal closure [59]. In all, it could be proposed that H₂S is involved in ABA-stimulated stomatal closure. Thus, MPK4 may act downstream of H₂S, and H₂S-MPK4 signal cascade is involved in ABA-stimulated stomatal closure in alleviating drought stress [57].

Osmotic stress adversely causes internal environmental disorder on account of the overproduction of ROS, which leads to a decrease in plant growth and productivity. Usually, plants resist osmotic stress by enhancing the antioxidant system and stimulating signal transductions [60]. Wheat could adjust itself to resisting osmotic stress by enhancing antioxidant systems and inducing H₂S biosynthesis [61]. Furthermore, exogenous ABA induced AsA-GSH cycle activity, but H₂S scavenger HT and synthesis inhibitor aminooxy acetic acid (AOA) reversed the activities mentioned above [61]. These results suggest that H₂S induced by exogenous ABA is a signal that triggers the up-regulation of the AsA-GSH cycle under osmotic stress. Obviously, H₂S takes part in ABA-related stomatal closure in response to different environmental stresses; however, the relationship between them is complicated (Figure 3).

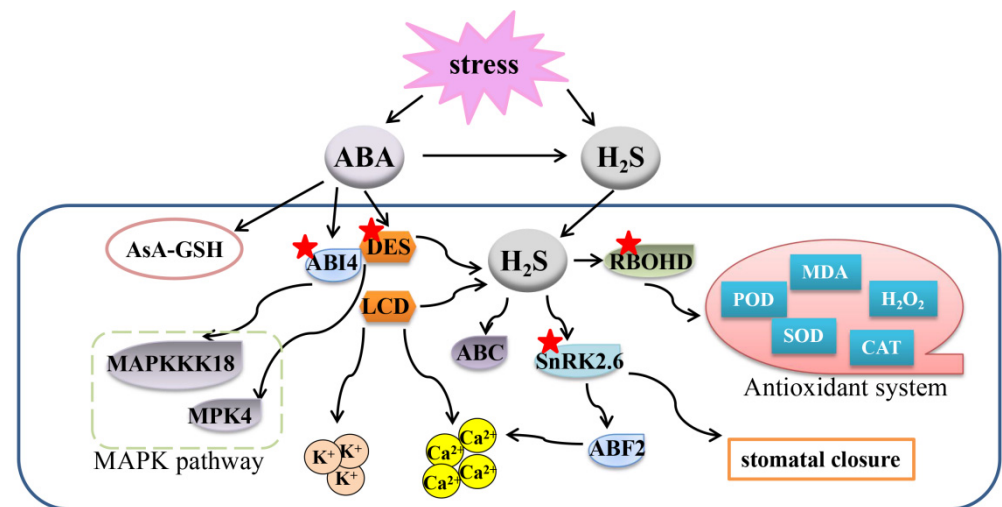


Figure 3. Overview of the mechanisms of the crosstalk between ABA and H₂S to regulate plant response to abiotic stresses. A gene or protein marked with a red asterisk means that the protein can be persulfidated. H₂S, hydrogen sulfide; ABA, abscisic acid; ABF2, ABA response element-binding factor 2; AsA-GSH, ascorbate-glutathione cycle; SnRK2.6, snf1-related protein kinase 2.6; RBOHD, respiratory burst oxidase homolog protein d; MDA, malondialdehyde, ABI4, abscisic acid insensitive 4; MAPK, mitogen-activated protein kinase.

3.2. Crosstalk between DES1/H₂S and ABA in Response to Drought Stress through Regulating Protein Persulfidation

ABA could stimulate H₂S generation under stresses, but how H₂S synthesis enzyme DES1 contributes to the crosstalk between ABA and H₂S is puzzled. Recently, by creating transgenic lines that expressed *DES1* in a tissue-specific pattern, it was found that the guard cell-specific *DES1* was involved in ABA-induced physiological molecular responses [62]. ABA-induced *DES1* expression and H₂S production in guard cells were inhibited by H₂S scavenger and restored by H₂S donor [62]. The above genetic and pharmacological evidence further confirmed the hypothesis that *DES1* is a unique component in ABA signaling in guard cells, and guard cell in situ *DES1*, together with H₂S, participates in ABA-guided stomatal closure [63].

Excitingly, another report discovered that the ABA signal was, in turn, commanded by H₂S-induced persulfidation of Open stomata 1 (OST1)/Snf1-related protein kinase 2.6 (SnRK2.6) on Cys131 and Cys137 residues in *A. thaliana* [64]. The persulfidated SnRK2.6 then interacted with ABA response element-binding factor 2 (ABF2), an ABA downstream protein, to modulate stomatal movement. Also, ABA was detected to induce *DES1* and *DCD* expressions within 5–30 min previously [63,65], which suggests that the accumulation of H₂S by ABA is ahead of the occurrence of protein persulfidation. Together with the works above, a hypothesis that ABA induces H₂S accumulation, which further persulfidates SnRK2.6 continuously to promote ABA signaling in guard cells, would be proposed. The persulfidated SnRK2.6 then enhanced ABA- and H₂S-induced Ca²⁺ influx, which subsequently caused stomatal closure through the inhibition of inward K⁺ channels and activation of outward anion channels [66]. To be encouraged continually, the *DES1*/H₂S-triggered persulfidation mechanism in ABA-regulated stomatal movement has been confirmed in another two reports [67,68]. One of their works found that ABA triggered *DES1* accumulation, and *DES1* auto-persulfidated at Cys44 and Cys205 in a redox-dependent fashion, causing a trigger of transient H₂S overproduction in guard cells [67]. They also found that the sustained *DES1*/H₂S drove persulfidation of the NADPH oxidase respiratory burst oxidase homolog protein d (RBOHD) at Cys825 and Cys890 to strengthen its ability to introduce a ROS burst, which in turn induced stomatal closure [67]. Together, this work suggests that H₂S-guided persulfidation of *DES1* and RBOHD may form a negative feedback loop that fine-tunes guard cell redox homeostasis and ABA signaling.

Abscisic acid insensitive 4 (ABI4) could also be persulfidated by DES1 at Cys250 in vitro and in vivo, and served as a downstream target of H₂S in plant's response to ABA under stress conditions [68]. In addition, DES1-linked persulfication of ABI4 induced *MPAKKK18* transactivation through binding to the CE1 motif in the *MAPKKK18* promoter, which further enlarged the MAPK signaling cascade induced by ABA. Meanwhile, ABI4 could bind to the *DES1* promoter and, in turn, activate its transcription, forming a DES1-ABI4 loop to fine-tune ABA-MAPK signals [68]. The results above illustrate a redox-based protein persulfidation mechanism within the crosstalk between H₂S- and ABA-involved stomatal movement [69]. Further work may focus on the molecular mechanisms of persulfidation and other post-translational modification events in H₂S-regulated ABA signaling in guard cells (Figure 3).

4. Crosstalk between H₂S and Ca²⁺ in Response to Abiotic Stresses

Ca²⁺ is another well-known second messenger in plant cells with the function of regulating intracellular physiological and biochemical processes, including alleviating abiotic stresses. Calmodulin (CaM) is a receptor protein in calcium signal transduction, and its main function is to perceive the volatility of intracellular calcium ions [10,70]. Recent studies uncovered a new signal transduction pattern in which Ca²⁺ and H₂S cooperate to help plants resist environmental stresses.

4.1. Crosstalk between H₂S and Ca²⁺ in Response to Heavy Metal Stress

Ca²⁺ influx was found to participate in restraining heavy metal contamination together with H₂S signal cascade. H₂S synthesis inhibitor and Ca²⁺ chelators aggravated the toxic phenotypes of foxtail millet (*Setaria italica*) exposed to Cr (VI) damage, demonstrating the involvement of H₂S and Ca²⁺ signals during this process [71]. Furthermore, Ca²⁺ enhanced the expressions of heavy metal chelator biosynthesis genes *Metallothionein-like type 3 (MT3A)* and *Phytochelatin Synthase (PCS)* and activated the antioxidant system, which was partially dependent on the H₂S signal [71], indicating a downstream role of H₂S in Ca²⁺ signaling. A later report in *A. thaliana* further discovered that the expression of H₂S synthesis enzyme LCD was increased through a Ca²⁺/calmodulin 2 (CaM2)-directed pathway, which may explain the generation of H₂S in the defense of plants against the Cr (VI) toxic condition [72,73]. The detailed mechanism was that the extracellular Cr (VI) stimulated Ca²⁺ influx, and the CaM2 protein then bound Ca²⁺ and interacted with the bZIP transcription factor TGA3, which further reinforced *LCD* gene expression and enhanced H₂S production [72]. Ca²⁺ and H₂S donor NaHS induced AsA-GSH cycle, redox homeostasis, and Ca²⁺-dependent protein kinase (CDPK) and *Phytochelatin* (*PCs*) genes expressions under Ni toxicity in zucchini seedlings [74]. In addition, H₂S scavenger HT inhibited H₂S accumulation induced by Ca²⁺, and Ca²⁺ chelator ethylene glycol-bis(b-aminoethylether)-N,N,N',N'-tetra-acetic acid (EGTA) eliminated the impacts of seed priming induced by NaHS [74]. Thus, Ca²⁺ and H₂S may manifest a two-side crosstalk in inoculating plants against heavy metal conditions. The relationship between NO and H₂S has been discussed in another part of the present article, and it was put forward that Ca²⁺, in association with NO and H₂S, improved chlorophyll metabolism, photosynthesis, carbohydrate accumulation, and maintained redox homeostasis in *Vigna radiata* under Cd stress [32]. The study also discovered that NO scavenger cPTIO could reduce Ca²⁺ content, and that EGTA reduced H₂S content and altered Ca²⁺-dependent LCD and DCD enzyme activities, but that HT could not considerably reduce Ca²⁺ content [32]. Therefore, Ca²⁺, as a downstream signal of NO, may act in a two-side crosstalk pattern with H₂S during plants' adjustment to heavy metal contamination (Figure 2).

4.2. Crosstalk between H₂S and Ca²⁺ in the Regulation of Stomatal Closure

Stomatal closure is an important physiological process under stress conditions; thus, the role of Ca²⁺ in stomatal closure was also summarized here. As mentioned above, H₂S contributed to regulate S-type anion channel activation in guard cells, and this process

was correlated with the SnRK2.6 function and the level of cytosolic free Ca^{2+} [59]. Further, H_2S induced the Ca^{2+} influx in guard cells by stimulating the accumulation of ROS [75]. H_2S triggered the persulfidation of SnRK2.6, and the persulfidated SnRK2.6 enhanced ABA- and H_2S -induced Ca^{2+} influx, which subsequently caused stomatal closure [64]. Therefore, Ca^{2+} may function downstream of H_2S -driven stomatal closure in a redox- and post-translational persulfidation-dependent manner (Figure 2).

4.3. Crosstalk between H_2S and Ca^{2+} in Response to Other Stresses

As signal messengers, the crosstalk between H_2S and Ca^{2+} has also been validated in many kinds of other stress conditions. Pretreating with H_2S enhanced the heat tolerance of tobacco (*Nicotiana tabacum* L.) suspension-cultured cells by inhibiting electrolyte leakage and MDA accumulation, and exogenous Ca^{2+} and its ionophore A23187 intensified these effects [76]. However, H_2S -induced heat tolerance was restrained by the application of Ca^{2+} chelator EGTA, as well as CaM antagonists chlorpromazine (CPZ) and trifluoperazine (TFP), illustrating a role of Ca^{2+} and CaM in H_2S -triggered heat tolerance [76]. Afterward, another study announced that exogenous H_2S enhanced the heat resistance of wheat coleoptiles through strengthening antioxidant enzyme activities in a Ca^{2+} -dependent manner [77]. Thus, Ca^{2+} and CaM participate in H_2S -induced heat tolerance in plants.

As for K^+ deficiency under NaCl stress in *Vigna radiata* seedlings, Ca^{2+} increased endogenous H_2S generation, and Ca^{2+} and H_2S then cooperated with each other to induce an Na^+/H^+ antiport system and antioxidant defense [78]. Considering another result that adding of Ca^{2+} -chelator EGTA and H_2S scavenger HT reversed the effects of Ca^{2+} [78], a hypothesis may be drawn that H_2S acts downstream during Ca^{2+} -mediated plant adaptive responses to NaCl stress (Figure 2).

5. Crosstalk between H_2S and H_2O_2 in Response to Abiotic Stresses

H_2O_2 is a colorless transparent liquid and crucial signaling molecule. Various studies have shown that H_2O_2 plays important roles in seed germination, stomatal movement, shoot and root development, pollination, and fruit ripening [79]. Also, it can modulate the plant growth and development under abiotic stresses [80]. The crosstalk between H_2S and H_2O_2 under stress has been studied in recent years.

5.1. Crosstalk between H_2S and H_2O_2 in Response to Heavy Metal Stress

Cd stress could regulate the homeostasis of ROS and promote oxidative injury, which may cause cell death [81]. Cd could decrease vacuolar H^+ -ATPase activity, which was able to generate a proton gradient across the vacuolar membrane [82]. Under high Cd concentration stress, H_2O_2 and $\text{O}_2^{\cdot-}$ significantly enhanced and triggered the oxidative injury, thus resulting in cell death in *Brassica rapa* root tips [81]. However, when *B. rapa* was exposed to low concentration Cd stress, the transcript levels of H_2S biosynthesis-related genes *LCD* and *DCD* were significantly increased. Simultaneously, H_2O_2 had a remarkable increase and $\text{O}_2^{\cdot-}$ went down, whereas H_2S biosynthesis inhibitor or H_2S scavenger reversed the positive effects, indicating a role of H_2S in alleviating low Cd stress by adjusting the balance between H_2O_2 and $\text{O}_2^{\cdot-}$ [81]. H_2S donor NaHS treatment increased the photosynthetic fluorescence parameters in cotyledons of cucumber (*C. sativus* L. var. Wisconsin) seedling roots exposed to 100 μM CdCl_2 for 24 h [82]. In addition, both the enhancement of H_2O_2 content and the decline in H_2S content in roots decreased vacuolar H^+ -ATPase activity under Cd stress. Further, the increase in H_2S content in root tissue by exogenous H_2O_2 had nothing to do with the desulfurization enzyme activity. Exogenous H_2S remarkably enhanced the NADPH oxidase activity and the relative gene expression; however, it did not have an effect on the accumulation of H_2O_2 in cucumber roots under Cd stress [82]. Hence, H_2S content might be partially enhanced through the H_2O_2 /NADPH oxidase-induced pathway, independent of desulfhydrase activity (Figure 4).

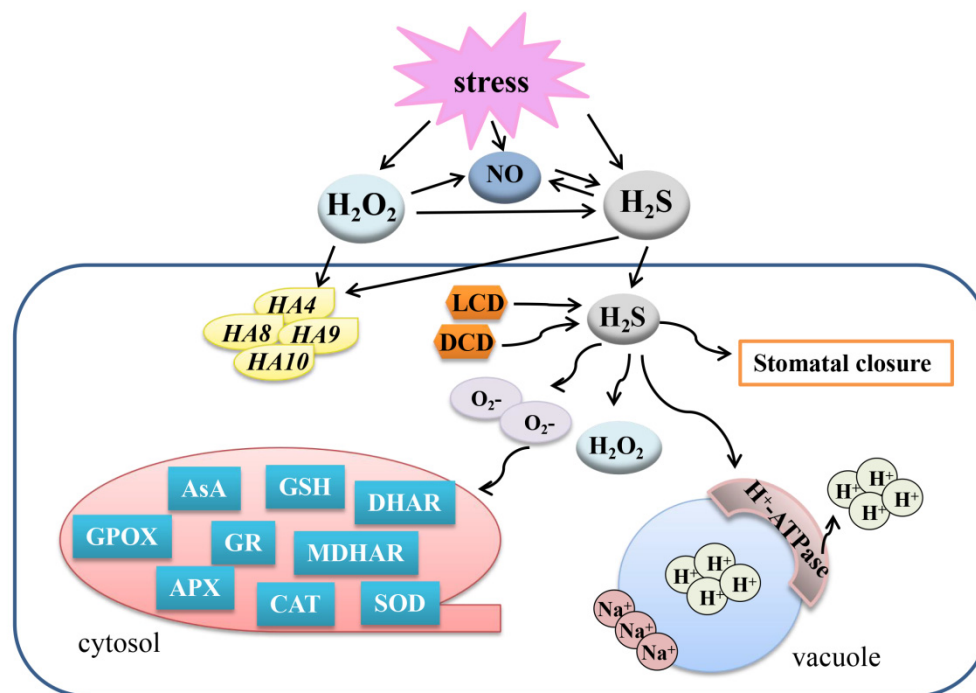


Figure 4. Overview of the mechanisms of the crosstalk between H₂S, NO, and H₂O₂ to regulate plant response to abiotic stresses. H₂S, hydrogen sulfide; H₂O₂, hydrogen peroxide; NO, nitric oxide; LCD, L-cysteine desulhydrase; DCD, D-cysteine desulhydrase; AsA, ascorbic acid; GSH, glutathione; GR, glutathione reductase; APX, ascorbate peroxidase; GPOX, guaiacol peroxidase; CAT, catalase; SOD, superoxide dismutase; DHAR, dehydroascorbate reductase; MDHAR, monodehydroascorbate reductase.

5.2. Crosstalk between H₂S and H₂O₂ in Response to Salt Stress

H₂S donor NaHS could enhance the activity of PM H⁺-ATPase under salt or low-temperature stress in cucumber, and the transcript levels of the plasma membrane proton pump-related genes including *CsHA2*, *CsH4*, *CsH8*, *CsH9*, and *CsHA10* were also increased [83]. However, NO and H₂O₂ only enhanced the expression of *CsHA1*. Therefore, H₂S, NO, and H₂O₂ could resist the salt stress by regulating the plasma membrane proton pump at different standards. Usually, salt stress could induce stomata closure. However, the H₂S scavengers HT, AOA, hydroxylamine (NH₂OH), potassium pyruvate (C₃H₃KO₃), ammonia (NH₃), H₂O₂, ascorbic acid (AsA), CAT, and diphenyl iodide (DPI) suppressed the closure of stomata in *V. faba* L. [44], suggesting that both H₂S and H₂O₂ could regulate stomatal movement under salt stress. Furthermore, endogenous H₂S and H₂O₂ accumulation and the activities of LCD and DCD were enhanced by salt treatment in guard cells. Nevertheless, these effects were inhibited by H₂O₂ and H₂S scavengers. Exogenous H₂O₂ scavengers prevented the increase in endogenous H₂S level as well as the stomatal closure; however, H₂O₂ generation was barely influenced with the application of H₂S scavengers in guard cells responding to salt stress [44]. Hence, H₂S may act as the downstream of H₂O₂-alleviated salt stress (Figure 4).

5.3. Crosstalk between H₂S and H₂O₂ in Response to Drought Stress

Drought stress is one of the most serious abiotic stresses in the world. Treatment by spermidine (Spd) remarkably enhanced H₂S production and activities of antioxidant enzymes [SOD, CAT, guaiacol peroxidase (GPOX), APX, GR, dehydroascorbate reductase (DHAR), and monodehydroascorbate reductase (MDHAR)] in white clover (*Trifolium repens*) under dehydration conditions [84]. Furthermore, NO and H₂S scavengers could not reduce the generation of H₂O₂ induced by Spd, but H₂O₂ scavengers could effectively inhibit the increase of NO and H₂S induced by Spd. The H₂S signal induced by Spd was

also significantly inhibited by NO scavenger [84]. Hence, in response to dehydration, H₂S may be the downstream signaling molecule to interact with NO and H₂O₂ (Figure 4).

5.4. Crosstalk between H₂S and H₂O₂ in Response to Other Stresses

UV-B is a common stress in practical agricultural production. When plants encounter the UV-B stress, the levels of electrolyte leakage, MDA, and ultraviolet absorbing compounds decreased, and the activities of antioxidant enzymes, GSH, and AsA also declined [85]. However, exogenous H₂S, H₂O₂, and putrescence (Put) could alleviate the negative effects of UV-B stress. The protective role of Put in UV-B radiation damage was reduced by the inhibitors of H₂S, H₂O₂, and Put [86]. Moreover, the level of H₂O₂ was increased by exogenous H₂S, and the enhanced H₂O₂ promoted the accumulation of UV absorbing compounds in hullless barley (*H. vulgare* L. var. nude, Kunlun-12) seedlings, thus preserving the steady state of oxidation-reduction under UV-B stress and improving its UV-B tolerance [86].

In addition, extreme temperature is a key factor which influences plant growth and development. H₂S, NO, and H₂O₂ had a significant impact in response to low temperature (10 °C) by modulating the plasma membrane proton pump in cucumber roots [83]. Moreover, H₂O₂ treatment could improve the heat resistance in maize (*Z. mays* L., Huidan No. 4) seedlings, and this effect could be strengthened by NO and H₂S donors but abolished by NO and H₂S scavengers or synthesis inhibitors [87]. It seems that NO and H₂S act downstream of H₂O₂ in the acquisition of heat resistance in plants (Figure 4).

6. Crosstalk between H₂S and Other Signal Molecules in Response to Abiotic Stresses

In recent years, many kinds of signal transmitters have emerged to regulate plant growth and development, and to acclimate to environment changes. The protective role of H₂S related to these signal molecules such as SA, ETH, JA, Pro, and MT (mentioned in another part of the article) under toxic environment in plants has also been explored to some extent.

6.1. Crosstalk between H₂S and SA in Response to Abiotic Stresses

SA has long been recognized as a pivotal signal messenger, manifesting multiple functions in defending plant disease and adverse environmental conditions. Endogenous SA biosynthesis is mainly proceeded in the cytoplasm through the phenylalanine route by phenylalanine ammonia lyase (PAL) and benzoic-acid-2-hydroxylase (BA2H) [10,88,89]. SA and H₂S enhanced heat tolerance by strengthening the activities of antioxidant enzymes and increasing osmolyte content in maize seedlings [90]. Further, SA induced endogenous H₂S generation by enhancing the activity of H₂S synthesis enzyme DES [91]. While the increase in SA production and the relative enzyme activities of PAL and BA2H were rarely influenced by H₂S, this downstream role of H₂S in SA-induced stress responses was also similarly reported in Cd tolerance in *A. thaliana* [92]. Thus, the positive role of SA under the stress condition is partially dependent on H₂S. Pb stress accelerated endogenous H₂S production [35]. Moreover, SA improved enzyme activities of the AsA-GSH cycle system in pepper under Pb stress [93]. In addition, exogenous SA enhanced the H₂S content, which was further reinforced by H₂S donor NaHS. It seems that SA triggers endogenous H₂S accumulation, which further regulates the AsA-GSH cycle to resist Pb toxicity (Figure 5).

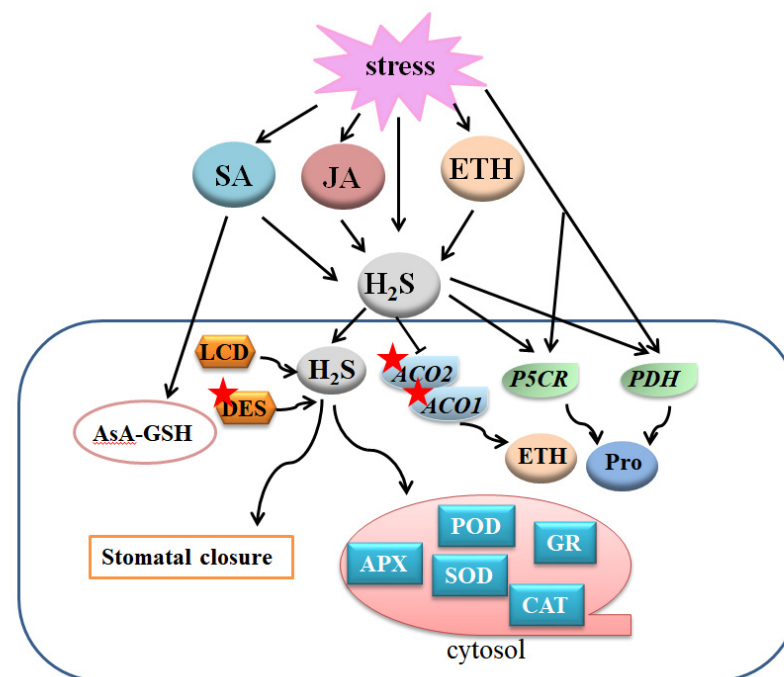


Figure 5. Overview of the mechanisms of the crosstalk between H₂S and JA, SA, ETH, and Pro to regulate plant response to abiotic stresses. A gene or protein marked with a red asterisk means that the protein can be persulfidated. H₂S, hydrogen sulfide; LCD, L-cysteine desulphydrase; DES, desulphydrase; SA, salicylic acid; JA, jasmonic acid; ETH, ethylene; Pro, proline; APX, ascorbate peroxidase; SOD, superoxide dismutase; GR, glutathione reductase; POD, peroxidase; CAT, catalase; ACO1, 1-aminocyclopropane-1-carboxylic acid oxidase 1; ACO2, 1-aminocyclopropane-1-carboxylic acid oxidase 2; P5CR, proline-5-carboxylate reductase; PDH, proline dehydrogenase.

6.2. Crosstalk between H₂S and ETH in Response to Abiotic Stresses

Ethylene induced H₂S biosynthesis in guard cells in tomatoes under osmotic stress [94]. Moreover, the effect of ethylene on resisting osmotic stress was reversed by H₂S scavenger HT or H₂S synthetic inhibitor PAG, suggesting a downstream component of H₂S in ethylene-triggered stomatal closure under osmotic stress. Further, H₂S induced the persulfidation of 1-aminocyclopropane-1-carboxylic acid oxidase1 (ACO1) and ACO2, and restrained their expressions. As a result, H₂S negatively regulated ethylene generation in response to osmotic stress [94]. These results are parallel with a recently published mechanism of waterlogging damage resistance in peach (*Prunus persica* L. Batsch) seedlings [95], in which H₂S restrained over-synthesis of ethylene as well as inhibited oxidative damage under waterlogging stress (Figure 5).

6.3. Crosstalk between H₂S and JA in Response to Abiotic Stresses

JA is another phytohormone kind signal transmitter with extensive modulation functions in plant root elongation [96], anthocyanin accumulation and trichome initiation [97], stamen development and flowering [98], leaf senescence [99], and stress resistance [100]. A recent study announced a critical role of JA in inhibiting stomatal development in *A. thaliana* [101]. Furthermore, JA positively modified LCD activity and H₂S production. The JA-deficient mutants represented a high stomatal density phenotype, which could be reversed by exogenous H₂S, whereas the H₂S synthesis-deficient mutants *lcd* displayed similar stomatal development phenotype as the JA-deficient mutants, which could be rescued by H₂S donor NaHS but not by JA [102]. Thus, H₂S may act as a downstream member of JA in stomatal development (Figure 5).

6.4. Crosstalk between H₂S and Pro in Response to Abiotic Stresses

Pro is a kind of organic osmolyte with a wide distribution in plant cells. Previous studies have demonstrated the increase of Pro after the application of signal transmitter agents in defense of abiotic stresses [89,103,104]. Pretreatment with exogenous H₂S increased endogenous Pro content, and the activities and transcription levels of proline-5-carboxylate reductase (P5CR) and proline dehydrogenase (PDH) in foxtail millet, whereas H₂S scavenger or inhibitor reduced the above effects [105]. Moreover, the combined application of H₂S and Pro resulted in preferable growth status, stomatal movement, and oxidative remission under stress conditions. These results indicate a cooperation of Pro and H₂S under adverse environments (Figure 5).

7. Conclusions and Outlook

The disadvantageous environment conditions cause oxidative damage, ionic imbalance, and osmotic stress to plants, resulting in a weakened growth and development status. H₂S can reinforce plant tolerance to these stresses through constructing a luxuriant crosstalk with other signal molecules, such as NO, ABA, Ca²⁺, H₂O₂, SA, ETH, JA, Pro, and MT. The genes regulated by H₂S and other molecules under abiotic stress conditions are displayed in Table 1. There exists a legible clue that environmental stresses and various signal transmitters stimulate endogenous H₂S generation and improve the activities of H₂S synthesis enzymes under the stress condition. Meanwhile, H₂S represents a feedback manner to enhance the signal cascades in inducing the accumulation of some signal messengers, especially NO, ABA, and Ca²⁺. In addition, the existence of DES1-related auto-persulfidation and persulfidation may be the reason for the extensive inspiration of its enzyme activity in different stress conditions. In summary, H₂S acts as a downstream signal member in cooperation with ABA, H₂O₂, SA, ETH, JA, and MT, but an upstream signal member of Pro under stress condition. Nevertheless, the crosstalk between H₂S, NO, and Ca²⁺ represents a two-side signal cascades manner, whereas relationships between H₂S and other signal molecules vary on account of the specific stress pattern.

Multiple types of research need to be done to explore the point-to-point mechanism within the crosstalk between H₂S and one single signal transducer under abiotic stress conditions. Firstly, the feedback molecular mechanism of H₂S and NO, and the interactions within protein persulfidation, S-sulfhydration, and S-nitrosylation, remain unclear. Next, more post-translational modification proteins need to be discovered and identified that are triggered by H₂S in ABA- or NO-dependent signal pathways under stress condition. Finally, new signal messengers related to H₂S activity are waiting to be discovered.

Table 1. Genes regulated by H₂S and other molecules under abiotic stress conditions.

Crosstalk between H ₂ S and other Molecules	Stresses	Plant Species	Tissue	Regulated Genes	References
H ₂ S and NO	salt stress	<i>Medicago sativa</i>	seeds	APX-1, APX-2, and Cu/Zn-SOD	[39]
		<i>Hordeum vulgare</i> L.	seedlings	HvHA, HvVHA-β, HvSOS1, HvVNHX2, HvAKT1 and HvHAK4	[22]
	drought hypoxia stress cadmium stress cobalt stress	<i>Solanum lycopersicum</i>	seedlings	SIL-DES, SICAS and SICS	[40]
		<i>M. sativa</i> L.	leaves	GST17, Cu/ZnSOD, FeSOD, NR, cAPX, PIP	[48]
		<i>Zea mays</i> L.	seedlings	P4H, ADH, CRT1, GS, CYP51 and ME	[43]
aluminum stress	<i>M. sativa</i> L.	seedlings	Cu/Zn-SOD, APX and POD	[31]	
	<i>Triticum aestivum</i> L.	seedlings	RbcL	[32]	
H ₂ S and ABA	drought	<i>Glycine max</i> L.	seedlings	MATE13, MATE47, MATE58, MATE74, MATE79, MATE84, and MATE87	[34]
		<i>Oryza sativa</i> L.	seedlings	NCED2, NCED3, NCED5, AREB1, AREB8, bZIP23 and LEA3	[54]
	chromium stress nickel stress	<i>Arabidopsis</i>	seedlings	TPC1, GORK, SKOR, KCO1, MYP5, ACA9, ACA11, CAX1, SLAC1, AKT1A, KT2, KCI and KAT1	[55]
		<i>T. aestivum</i> L.	leaves and roots	TaZEP, TaNCED, TaAAO and TaSDR	[56]
		<i>Arabidopsis thaliana</i>	-	MAPKs	[57]
H ₂ S and Ca ²⁺	chromium stress	<i>A. thaliana</i>	seedlings	LCD	[72]
		<i>Cucurbita pepo</i> L.	seedlings	CDPK and PCS1	[74]
	<i>Setaria italica</i>	seedlings	MT3A, PCS, CaM, CBL and CDPK	[71]	
H ₂ S-H ₂ O ₂	cadmium stress	<i>Brassica rapa</i> .	seedlings	Br_UPB1A, Br_UPB1B; Bra035235, Bra033551, Bra006423, ra023639	[89]
				CsVHA-A, CsVHA-B, CsVHA-a1, CsVHA-a2, CsVHA-a3, CsVHA-c1, CsVHA-c2 and CsVHA-c3	[82]

Table 1. Cont.

Crosstalk between H ₂ S and other Molecules	Stresses	Plant Species	Tissue	Regulated Genes	References
H ₂ S, NO and H ₂ O ₂	salt or low temperature	<i>C. sativus</i> L.	roots	<i>CsHA1, CsHA2, CsH4, CsH8, CsH9</i> and <i>CsHA10</i>	[83]
	dehydration	<i>Trifolium repens</i>	seedlings	<i>bZIP37, bZIP107, DREB2, DREB4</i> and <i>WRKY108715</i>	[84]
H ₂ S and ETH H ₂ S and Pro	osmotic stress	<i>S. lycopersicum</i>	seedlings	<i>LeACO1</i> and <i>LeACO2</i>	[94]
	cadmium stress	Foxtail millet	seedlings	<i>PDH</i> and <i>P5CR</i>	[105]

APX, ascorbate peroxidase; SOD, superoxide dismutase; HA, H⁺-ATPase; VNHX2, vacuolar Na⁺/H⁺ antiporter; VHA-β, H⁺-ATPase subunit β; HAK4, high-affinity K⁺ uptake system; L-DES, L-cysteine desulphydrase; CAS, β-cyanoalanine synthase; CS, L-cysteine synthase; P4H, prolyl 4-hydroxylase; ADH, alcohol dehydrogenase; CRT1, calcium binding protein; CYP51, cytochrome P450 14a-sterol demethylase; GS, glutamate synthase 1; ME, NADP-dependent malic enzyme; POD, peroxidase; rbcL, rubisco large subunit; NCED, 9'-cis-epoxycarotenoid dioxygenase; TPC1, two pore segment channel 1; GORK, guard cell outward-rectifying K⁺ channel; SKOR, SKI family transcriptional corepressor; KCO, outward-rectifying K⁺ channel; ACA, adenylyl cyclase-associated protein; CAX, calcium exchanger; SLAC1, slow anion channel associated 1; AKT, *Arabidopsis* potassium transporter; KC1, potassium channel 1; KAT1, potassium channel in *Arabidopsis thaliana* 1; ZEP, zeaxanthin epoxidase; AAO, abscisic aldehyde oxidase; SDR, short-chain dehydrogenase; MAPK, mitogen-activated protein kinase; LCD, L-cysteine desulphydrase; CDPK, Ca²⁺-dependent protein kinase; PCS, phytochelatin; CaM, calmodulin; CBL, calcineurin B-like; ACO, 1-aminocyclopropane-1-carboxylic oxidase; PDH, proline dehydrogenase; P5CR, proline-5-carboxylate reductase.

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