



Hydrogen Sulfide: A Signal Molecule in Plant Cross-Adaptation

Zhong-Guang Li^{1,2,3*}, Xiong Min^{1,2,3} and Zhi-Hao Zhou^{1,2,3}

¹ School of Life Sciences, Yunnan Normal University, Kunming, China, ² Engineering Research Center of Sustainable Development and Utilization of Biomass Energy, Ministry of Education, Kunming, China, ³ Key Laboratory of Biomass Energy and Environmental Biotechnology, Yunnan Normal University, Kunming, China

For a long time, hydrogen sulfide (H₂S) has been considered as merely a toxic by product of cell metabolism, but nowadays is emerging as a novel gaseous signal molecule, which participates in seed germination, plant growth and development, as well as the acquisition of stress tolerance including cross-adaptation in plants. Cross-adaptation, widely existing in nature, is the phenomenon in which plants expose to a moderate stress can induce the resistance to other stresses. The mechanism of cross-adaptation is involved in a complex signal network consisting of many second messengers such as Ca²⁺, abscisic acid, hydrogen peroxide and nitric oxide, as well as their crosstalk. The cross-adaptation signaling is commonly triggered by moderate environmental stress or exogenous application of signal molecules or their donors, which in turn induces cross-adaptation by enhancing antioxidant system activity, accumulating osmolytes, synthesizing heat shock proteins, as well as maintaining ion and nutrient balance. In this review, based on the current knowledge on H₂S and cross-adaptation in plant biology, H₂S homeostasis in plant cells under normal growth conditions; H₂S signaling triggered by abiotic stress; and H₂S-induced cross-adaptation to heavy metal, salt, drought, cold, heat, and flooding stress were summarized, and concluded that H₂S might be a candidate signal molecule in plant cross-adaptation. In addition, future research direction also has been proposed.

Keywords: cross-adaptation, hydrogen sulfide, signal crosstalk, stress tolerance

OPEN ACCESS

Edited by:

Hanjo A. Hellmann,
Washington State University, USA

Reviewed by:

Karl-Josef Dietz,
Bielefeld University, Germany
Sutton Mooney,
Washington State University, USA

*Correspondence:

Zhong-Guang Li
zhongguang_li@163.com

Specialty section:

This article was submitted to
Plant Physiology,
a section of the journal
Frontiers in Plant Science

Received: 07 May 2016

Accepted: 13 October 2016

Published: 26 October 2016

Citation:

Li Z-G, Min X and Zhou Z-H (2016)
Hydrogen Sulfide: A Signal Molecule
in Plant Cross-Adaptation.
Front. Plant Sci. 7:1621.
doi: 10.3389/fpls.2016.01621

INTRODUCTION

Cross-adaptation, widely existing in nature, is the phenomenon in which plants expose to a moderate stress can induce the resistance to other stresses (Li and Gong, 2011; Foyer et al., 2016; Hossain et al., 2016). For example, cold pretreatment can improve the heat tolerance of winter rye, salt shock can rapidly induce the cold tolerance in spinach and potato, ultraviolet radiation (UV-B) can enhance the heat tolerance in cucumber and the cold tolerance in *Rhododendron*, and mechanical stimulation can improve the heat tolerance and the chilling tolerance in tobacco cells (Knight, 2000; Li and Gong, 2011, 2013). Interestingly, Foyer et al. (2016) found that cross-adaptation also can be induced between abiotic and biotic stresses. Infection by mycorrhizal fungi can improve the resistance of tomato, sunflower, pea, and rice to drought, chilling, salinity, metal toxicity, and high temperature stress (Grover et al., 2011), while drought stress can reduce aphid fecundity in *Arabidopsis* (Pineda et al., 2016). Our previous work also showed that heat shock could improve the resistance of maize seedlings to heat, chilling, salt, and drought stress (Gong et al., 2001). Numerous studies found that the acquisition of stress tolerance including cross-adaptation

was involved in a complex signal network consisting of many second messengers such as Ca²⁺, abscisic acid (ABA), hydrogen peroxide (H₂O₂) and nitric oxide (NO), as well as their crosstalk (Knight, 2000; Pandey, 2015; Li and Gu, 2016; Li and Jin, 2016; Niu and Liao, 2016; Wang et al., 2016). In tobacco, mechanical stimulation can successively trigger H₂O₂ and NO signaling (Li and Gong, 2011, 2013), heat shock can induce Ca²⁺ and ABA signaling one after the other (Gong et al., 1998a,b), which in turn induce cross-adaptation to heat and chilling stress, similar results were reported by Gong et al. (2001) in maize seedlings. These results indicate that the acquisition of cross-adaptation is involved in signal crosstalk among Ca²⁺, H₂O₂, NO, and ABA in plants. Recently, hydrogen sulfide (H₂S) was also found to be a member of this signal network in plants (Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014; Fotopoulos et al., 2015; Guo et al., 2016), indicating that H₂S might be a signal molecule in plant cross-adaptation.

For a long time, H₂S has been considered as merely a toxic intermediate of cell metabolism due to its strong affinity to Fe²⁺-containing proteins such as cytochrome oxidase, hemoglobin and myoglobin, which may have been primary cause of the mass extinction of species in the Permian (Li, 2013; Lisjak et al., 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014; Fotopoulos et al., 2015; Guo et al., 2016; Yamasaki and Cohen, 2016). H₂S can inhibit oxygen release from young seedlings of six rice cultivars (Bluebelle, Dawn, Norin 22, Saturn, Yubae, and Zenith) and nutrient uptake such as phosphorus (Li, 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014). But nowadays, H₂S is found to function as gaseous signal molecule at low concentration similar to carbon monoxide (CO) and NO in plants, and it has been shown that plants can actively synthesize endogenous H₂S under normal, especially biotic or abiotic stress conditions (Li, 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014; Yamasaki and Cohen, 2016). The accumulation of endogenous H₂S has become a common response of plants to environmental stress, including salt, heavy metal (HM), drought, heat and cold stress, as well as pathogen infection, which may be closely associated with the acquisition of stress tolerance in plants (Li, 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014). More interestingly, exogenously applied H₂S, releasing from its donors such as NaHS and morpholin-4-ium 4-methoxyphenyl(morpholino) phosphinodithioate (GYY4137), shows significant positive effects on seed germination (Li et al., 2012a; Li and He, 2015; Wojtyła et al., 2016), organogenesis and growth (Lin et al., 2012; Fang T. et al., 2014), the regulation of senescence (Zhang et al., 2011), as well as the acquisition of stress tolerance such as salt (Christou et al., 2013), HM (Chen et al., 2013), drought (Christou et al., 2013), heat (Li et al., 2013a,b; Li, 2015c) and cold tolerance (Fu et al., 2013). These results indicate that H₂S may be a candidate signal molecule in plant cross-adaptation. In addition, NaHS and GYY4137 are commonly used as H₂S donors because they can release H₂S when dissolved in water, but NaHS giving a relatively short burst of H₂S, while GYY4137 giving a longer more prolonged exposure to H₂S (Wang, 2012; Lisjak et al., 2013). However, whether H₂S concentration in plant

cells or tissues is consistent with that of NaHS and GYY4137 applied as well as actual H₂S concentration triggering cross-adaptation need to be further investigated. In addition, H₂S usually exist in the forms of H₂S (approximately 20%) and HS⁻ (approximately 80%) in water solution, exact physiological concentration of H₂S in plant cells or subcellular organelles is not clear.

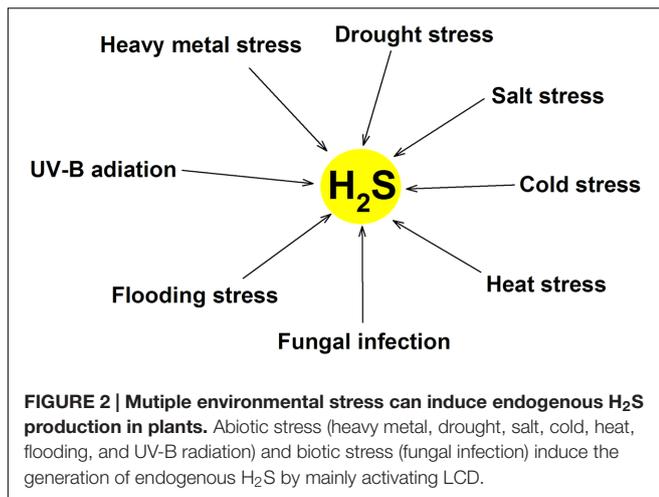
Though, there are a lot of excellent reviews which expound potential physiological function of H₂S in seed germination, plant growth and development, as well as the acquisition of stress tolerance (Li, 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014, 2016; Jin and Pei, 2015; Guo et al., 2016; Scuffi et al., 2016; Yamasaki and Cohen, 2016), the role of H₂S as a candidate signal molecule in plant cross-adaptation was not summarized in depth. Therefore, in this review, H₂S homeostasis in plant cells under normal growth conditions, H₂S signaling triggered by adverse environment and H₂S-induced cross-adaptation to various abiotic stresses are summarized, which further uncovers that H₂S may be a candidate signal molecule in plant cross-adaptation.

H₂S HOMEOSTASIS IN PLANT CELLS

As mentioned above, due to the dual role of H₂S, that is, as cytotoxin at high concentration and as cell signal molecule at low concentration, H₂S homeostasis in plant cells is very important to exert its physiological functions including cross-adaptation induction. In plant cells, there are many metabolic pathways to regulate H₂S homeostasis, similar to other signal molecules like H₂O₂, NO. H₂S homeostasis is closely regulated by L-cysteine desulfhydrase (LCD, EC 4.4.1.1), D-cysteine desulfhydrase (DCD, EC 4.4.1.15), sulfite reductase (SiR, EC 1.8.7.1), cyanoalanine synthase (CAS, EC 4.4.1.9), and cysteine synthase (CS, EC 4.2.99.8; Li, 2013, 2015a; **Figure 1**). LCD/DCD catalyzes the degradation of L-/D-cysteine to produce H₂S, amine and pyruvate; SiR reduces sulfite to H₂S using ferredoxin as electron donor; H₂S can be released from cysteine in the present of hydrogen cyanide by CAS; CS, namely O-acetyl-(thiol)-serine lyase (OAS-TL), can incorporate H₂S into O-acetyl-L-serine to form cysteine, and its reverse reaction can release H₂S (Li, 2013, 2015a; **Figure 1**). Generally, plants synthesize H₂S via LCD or DCD, which respond to environment stress and induce the acquisition of stress tolerance. In addition, excess H₂S can be released to air (Li, 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014).

H₂S SIGNALING TRIGGERED BY ABIOTIC STRESS

Similar to other second messengers such as Ca²⁺, H₂O₂, ABA and NO, the rapid production of endogenous H₂S in many species of plant can be triggered by numerous stresses (**Table 1**; **Figure 2**), this is a common response of plants to various abiotic stresses, which is closely associated with the acquisition of cross-adaptation in plants.



endogenous H₂S production (from 30 to 70 nmol g⁻¹ FW) (Lai et al., 2014). Exposure of strawberry seedlings to salinity (100 mM NaCl) and non-ionic osmotic stress (10% PEG-6000) greatly enhanced H₂S concentration (48 and 50 nmol g⁻¹ FW) in leaves, while 0.1 mM NaHS-pretreated plants subsequently exposed for 7 days to both stress factors were found to accumulate significantly higher amounts of H₂S (55 nmol g⁻¹ FW) in their leaves compared with NaCl-stressed plants (Christou et al., 2013).

H₂S Signaling Triggered by Drought Stress

One of the most severe abiotic stresses being experienced worldwide is drought. In *Arabidopsis* seedlings, the results of Shen et al. (2013) showed that treating wild type with polyethylene glycol (PEG) 8000, to simulate drought stress, caused an increase in production rate of endogenous H₂S (0.8 nmol mg⁻¹ protein min⁻¹). At early stage of osmotic exposure (PEG 6000 for 2 days), the endogenous H₂S in wheat seeds rapidly increased from 1.5 to 3.5 μmol g⁻¹ dry weight (DW) (Zhang et al., 2010a).

H₂S Signaling Triggered by Low Temperature Stress

Low temperature is a major environmental stress factors that limit plant growth, development and distribution. In grape (*Vitis vinifera* L.) seedlings, chilling stress at 4°C induced the expression of L/DCA genes and increased the activities of L/DCA, which in turn enhanced endogenous H₂S accumulation (from 7 to 15 μmol g⁻¹ FW) (Fu et al., 2013). Similarly, Shi et al. (2013) also found that cold stress treatment at 4°C could induce the accumulation of endogenous H₂S level (14 nmol g⁻¹ FW) in bermudagrass [*Cynodon dactylon* (L.) Pers.] seedlings. To uncover the adaptive strategies of alpine plants to the extremely cold conditions prevailing at high altitudes, Ma et al. (2015), using a comparative proteomics, investigated the dynamic patterns of protein expression in *Lamiophlomis rotata* plants grown at three different altitudes (4350, 4,800, and 5,200 m), and the results showed that the levels and enzyme activities of proteins (OAS-TL, CAS, L/DCA)

involved in H₂S biosynthesis markedly increased at higher altitudes (4,800 and 5,200 m), and that H₂S accumulation increased to 12, 22, and 24 nmol g⁻¹ FW, respectively, demonstrating that H₂S plays a central role during the adaptation of *L. rotata* to environmental stress at higher altitudes.

H₂S Signaling Triggered by High Temperature Stress

Similar to other stresses, high temperature also can induce endogenous H₂S generation in many species of plant. In 3-week-old seedlings of tobacco, Chen et al. (2016) found that treatment with high temperature at 35°C increased the activity of LCD, which in turn induced the production of endogenous H₂S (8 nmol g⁻¹ FW) in tobacco seedlings, and that H₂S production remained elevated level after 3 days of high temperature exposure. More interestingly, H₂S production by high temperature can induce the accumulation of jasmonic acid, followed by promoting nicotine synthesis. These data suggest that H₂S and nicotine biosynthesis is linked in tobacco plants subjected to high temperature stress. Additionally, heat stress caused a marked modulation in H₂S content in strawberry seedlings, as indicated in a significant increase after 1, 4, and 8 h of exposure to 42°C compared with control plants. A significant increase in H₂S content was also observed in 0.1 mM NaHS-pretreated plants after 1 h exposure to heat stress, gradually lowering to control levels thereafter (Christou et al., 2014).

H₂S Signaling Triggered by UV-B Radiation

Recently, Li et al. (2016) found that UV-B radiation could induce H₂S production in leaves of barley seedlings, reaching a peak of approximately 230 nmol g⁻¹ FW after 12 h of exposure, which in turn promoted the accumulation of UV-absorbing compounds flavonoids and anthocyanins. H₂S began to decline with time, but it is overall significantly higher than that of the control (approximately 125 nmol g⁻¹ FW) at 48 h of exposure. A similar trend was observed for LCD activity, which was corroborated by the application of DL-propargylglycine (PAG, an inhibitor of LCD) that resulted in complete inhibition of the H₂S production and the accumulation of UV-absorbing compounds induced by UV-B radiation (Li et al., 2016).

H₂S Signaling Triggered by Hypoxia and Fungal Infection

Flooding often leads to hypoxia in plant roots, which significantly limits agriculture production. In pea (*Pisum sativum* L.) seedlings, Cheng et al. (2013) found that hypoxia could activate H₂S biosynthesis system (LCD, DCA, OAS-TL, and CS), which in turn induced the accumulation of endogenous H₂S from approximately 0.9 (control) to 5.1 μmol g⁻¹ FW (hypoxia for 24 h), indicating that H₂S might be a hypoxia signaling that triggers the tolerance of the pea seedlings to hypoxic stress, this hypothesis was further supported by exogenously applied NaHS.

Pathogen infection is a common biotic stress in plants. In oilseed rape (*Brassica napus* L.) seedlings, fungal infection with *Sclerotinia sclerotiorum* led to an even stronger increase in H₂S, reaching a maximum of 3.25 nmol g⁻¹ DW min⁻¹ 2 days after infection, suggesting that the release of H₂S seems to be part of the response to fungal infection (Bloem et al., 2012).

H₂S Signaling Triggered by Exogenously Applied NaHS or Up-regulating the Expression of L/DCD

In addition to above-described abiotic and biotic stressors, H₂S signaling in plant cells also can be triggered by exogenously applying NaHS (H₂S donor) or up-regulating the expression of genes involved in H₂S biosynthesis like L/DCD under normal growth conditions. In strawberry seedlings, treatment of root with 0.1 mM NaHS resulted in significantly elevated H₂S concentration (35 nmol g⁻¹ FW) in leaves compared with control plants (25 nmol g⁻¹ FW) (Christou et al., 2013). In wheat seeds, the endogenous H₂S level [4.5 μmol g⁻¹ dry weight (DW)] in NaHS-treated seed was slightly higher than that of control (1.7 mol g⁻¹ DW) (Zhang et al., 2010a). These results indicated that H₂S is easy to enter into plant cells and follow on being transported to other tissues or organs due to its highly lipophilic property, which in turn exert its physiological role in plants.

Additionally, Jin et al. (2011) found that the *Arabidopsis* seedlings expressing L/DCD showed higher endogenous H₂S content under both normal (6 nmol mg⁻¹ protein min⁻¹) and drought stress conditions (14 nmol mg⁻¹ protein min⁻¹) compared with the control (3 nmol mg⁻¹ protein min⁻¹), and the expression pattern of L/DCD was similar to the drought associated genes dehydration-responsive element-binding proteins (*DREB2A*, *DREB2B*, *CBF4*, and *RD29A*) induced by dehydration, while exogenous application of H₂S (80 μM) was also found to stimulate further the expression of drought associated genes. In addition, drought stress significantly induced endogenous H₂S production in both transgenic plant and wild type, a process that was reversed by re-watering (Jin et al., 2011). Interestingly, *Arabidopsis* seedlings overexpressing LCD or pre-treated with NaHS exhibited higher endogenous H₂S level (from 2 to 10 nmol g⁻¹ FW), followed by improving abiotic stress (drought, salt, and chilling) tolerance and biotic stress (bacteria) resistance, while LCD knockdown plants or HT (H₂S scavenger) pre-treated plants displayed lower endogenous H₂S level and decreased stress resistance (Shi et al., 2015).

In conclusion, above-mentioned researches in this section display that: (1) under normal growth conditions, the content of endogenous H₂S or production rate in various plant species are different, ranging from 2 nmol g⁻¹ FW to 7 μmol g⁻¹ FW or 0.38 to 6 nmol mg⁻¹ protein min⁻¹. These differences may be relative to measurement methods, plant species and development stage, and experiment system. (2) Under abiotic stress conditions, the level of endogenous H₂S in various plant species is averagely increased by 2~2.5-fold, indicating that different environment stresses can trigger the H₂S signaling, which may be a trigger that induces the acquisition of cross-adaptation in plants.

H₂S-INDUCED CROSS-ADAPTATION

As described above, not only there are a broad range of environmental stressors can trigger H₂S signaling in plants, but pretreating plants with exogenously applied H₂S can provide additional resistance to subsequent stress exposure. The next section explores the role of H₂S as an important signaling molecule for cross-adaptation to HM, salt, drought, cold, heat and flooding stress by enhancing antioxidant system activity, accumulating osmolyte, synthesizing heat shock proteins (HSPs), as well as maintaining ion and nutrient balance (Table 2; Figure 3), which may be common mechanism of cross-adaptation induced by H₂S.

H₂S-Induced Metal and Metalloid Tolerance

Heavy metals refer to a group of metal elements with a density greater than 6 g/cm³, including Cr, Cu, Zn, and so forth (Gupta et al., 2013; Ahmad, 2016). Due to their toxicity and stability, HM has become the major abiotic stress in plants, and even threatens human health by way of the food chain. HM stress commonly results in oxidative stress, that is, the excessive accumulation of ROS, which leads to lipid peroxidation, protein oxidation, enzyme inactivation, and DNA damage (Yadav, 2010; Gupta et al., 2013; Ahmad, 2016). However, higher plants have evolved a sophisticated antioxidant defense system to scavenge excessive ROS and maintain its homeostasis in plants (Foyer and Noctor, 2009, 2011).

Arsenic (As) is a highly toxic metalloid, it is major pollutant in the soil. In pea seedlings, As treatment increased the accumulation of ROS, which in turn damage to lipids, proteins and biomembranes. Meanwhile, higher cysteine level was observed in As-stress seedlings in comparison to all other treatments (As-free; NaHS; As + NaHS), while these effects were alleviated by the addition of NaHS (Singh et al., 2015). Further experiments showed that As treatment inhibited the activity of the enzymes involved in the ascorbic acid (AsA)-glutathione (GSH) cycle, whereas their activities were enhanced by application of NaHS (Singh et al., 2015). In addition, the redox status of AsA and GSH was disturbed, as indicated by a steep decline in their reduced/oxidized ratios. However, exogenously applied NaHS restored the redox status of the AsA and GSH pools under As stress (Singh et al., 2015). Furthermore, NaHS treatment ameliorated As toxicity, which was coincided with the increased accumulation of H₂S. The results demonstrated that H₂S might counterbalance ROS-mediated damage to macromolecules by reducing the accumulation of As and triggering up-regulation of the AsA-GSH cycle, further suggesting that H₂S plays a crucial role in plant priming, and in particular for pea seedlings in mitigating As stress.

Under Cr stress, exogenous application of NaHS could improve the germination rate of wheat seeds in a dose-dependent manner and the activities of amylase, esterase as well as antioxidant enzymes superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione peroxidase

TABLE 2 | NaHS (H₂S donor)-induced cross-adaptation in plants.

Species	Tolerance	NaHS (mM)	Responsible factors	Reference
Pea	As	0.1	AsA–GSH cycle, reducing As accumulation	Singh et al., 2015
Wheat	Cr	1.2	Activating antioxidant enzymes	Zhang et al., 2010b
Wheat	Cu	1.4	Promoting amylase and esterase activities, maintain plasma membrane integrity	Zhang et al., 2008
Wheat	Al	0.6	Decreasing Al accumulation, alleviating citrate secretion, and oxidative stress	Zhang et al., 2010c
Barley	Al	0.2	Decreasing Al accumulation, alleviating citrate secretion, and oxidative stress	Chen et al., 2013
<i>Solanum nigrum</i>	Zn	0.2	Enhancing the metallothioneins, alleviating oxidative stress, reducing Zn uptake	Liu et al., 2016
Wheat	Salt	0.05	Promoting amylase and esterase activities	Bao et al., 2011
Alfalfa	Salt	0.1	Activating antioxidant enzyme	Wang et al., 2012
<i>Arabidopsis</i>	Salt	0.2	Maintaining a lower Na ⁺ /K ⁺ ratio, promoting the genes expression and the phosphorylation of H ⁺ -ATPase and Na ⁺ /H ⁺ antiporter	Li J. et al., 2014
Wheat	PEG-6000	0.6	Increasing CAT and APX activities, reducing lipoxygenase activity	Zhang et al., 2010d
Wheat	PEG-6000	1.0	Increased antioxidant enzymes activities and gamma-glutamylcysteine synthetase	Shan et al., 2011
<i>Arabidopsis</i>	Drought	0.08	Stimulating the expression of drought associated genes	Jin et al., 2011
<i>Vicia faba</i>	Drought	0.1	Increasing relative water content	García-Mata and Lamattina, 2010
Bermudagrass	Cold	0.5	Modulating antioxidant enzymes and non-enzymatic antioxidant	Shi et al., 2013
Grape	Cold	0.1	Enhancing SOD activity and the expression of VvICE1 and VvCBF3 genes	Fu et al., 2013
<i>Arabidopsis</i>	Cold	0.1	Up-regulating the transcripts of multiple abiotic and biotic stress-related genes	Shi et al., 2015
<i>Lamiophlomis rotata</i>	Cold	0.05	Increasing antioxidant enzyme activity, proline and sugar accumulation	Ma et al., 2015
Banana	Cold	0.5	Increasing the phenylalanine ammonia lyase activity, total phenolics content and antioxidant capacity	Luo et al., 2015
Strawberry	Heat	0.1	Maintaining ascorbate/glutathione homeostasis, inducing gene expression of enzymatic antioxidants, HSPs and aquaporins	Christou et al., 2014
Maize	Heat	0.7	Increasing antioxidant activity	Li Z.G. et al., 2014
Maize	Heat	0.5	Inducing proline accumulation	Li and Gong, 2013; Li et al., 2013a
Tobacco	Heat	0.05	Increasing antioxidant activity	Li et al., 2012b, 2015
Pea	Hypoxia	0.1	Protecting ROS damage, inhibiting ethylene production	Cheng et al., 2013

(GPX), whereas reduced the activity of lipoxygenase and over-production of malondialdehyde (MDA) as well as H₂O₂ induced by Cr, and sustained higher endogenous H₂S level (Zhang et al., 2010b). Additionally, NaHS pretreatment increased the activities of SOD and CAT, but decreased that of lipoxygenase in wheat under Cu stress (Zhang et al., 2008), these results were consisted with the response of wheat to Cr stress (Zhang et al., 2010b).

Also, NaHS could alleviate the inhibitory effect of Cu stress in wheat in a dose-dependent manner, and H₂S or HS⁻ derived from NaHS rather than other sulfur-containing components (S²⁻, SO₄²⁻, SO₃²⁻, HSO₄⁻, and HSO₃⁻) attribute to the potential role in promoting seed germination under Cu stress (Zhang et al., 2008). Further experiments showed that NaHS could increase amylase and esterase activities, reduced the disturbance of plasma membrane integrity induced by Cu in the radicle tips, and sustain lower MDA and H₂O₂ levels in germinating seeds (Zhang et al., 2008), similar to the reports by (Zhang et al., 2010b).

Aluminium (Al), a non-essential element for plants, adversely affects plant growth, development and survival, especially in acid soil. In barley (*Hordeum vulgare* L.) seedlings, Al stress inhibited the elongation of roots, while pretreatment

with NaHS partially rescued the inhibition of root elongation induced by Al, and this rescue was closely correlated with the decrease of Al accumulation in seedlings (Chen et al., 2013). Additionally, application of NaHS significantly alleviated citrate secretion and oxidative stress (as indicated in lipid peroxidation as well as ROS burst) induced by Al by activating the antioxidant system (Chen et al., 2013). Similar results were reported by Zhang et al. (2010c) in wheat (*Triticum aestivum* L.).

Though zinc (Zn) is an essential element for plants, its toxic effects can be observed when being excessive accumulation in plants. In *Solanum nigrum* L. seedlings, H₂S ameliorated the inhibition of growth by excess Zn, especially in roots, and an increase in free cytosolic Zn²⁺ content in roots, which was correlated well with the down-regulation of Zn uptake and homeostasis related genes expression like zinc-regulated transporter (ZRT), iron-regulated transporter (IRT)-like protein (ZIP) and natural resistance associated macrophage protein (NRAMP) (Liu et al., 2016). In addition, H₂S further enhanced the expression of the metallothioneins to chelate excessive Zn and alleviated Zn-oxidative stress by regulating the genes expression of antioxidant enzymes (Liu et al., 2016).

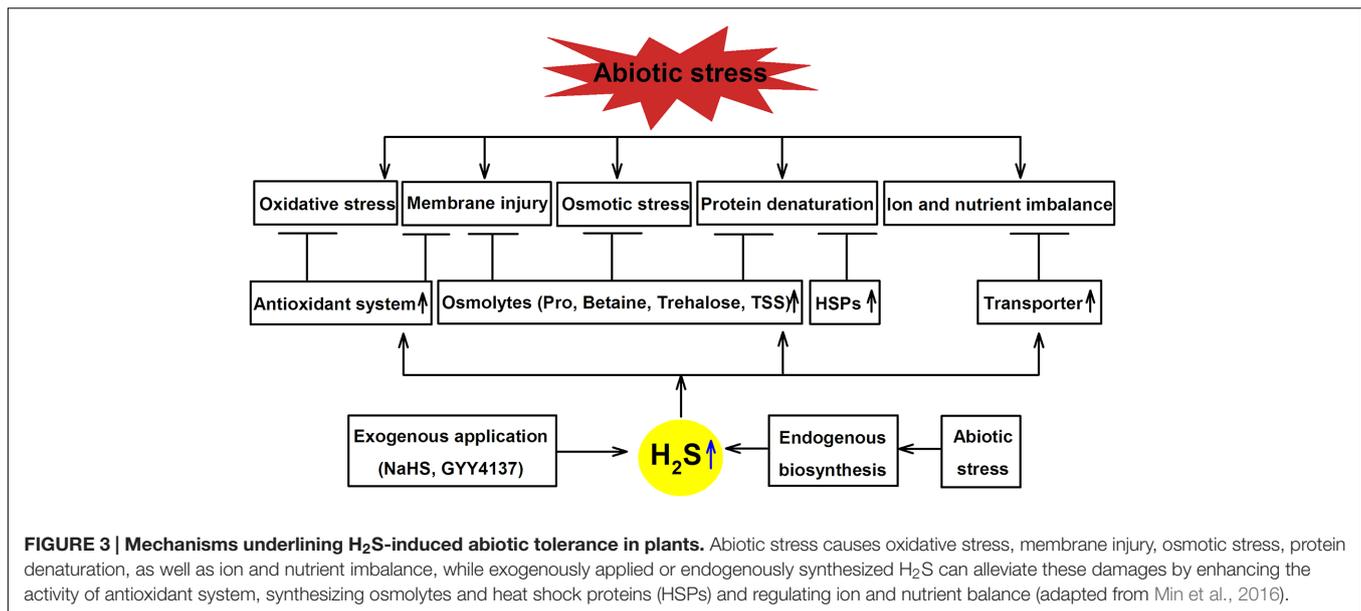


FIGURE 3 | Mechanisms underlying H₂S-induced abiotic tolerance in plants. Abiotic stress causes oxidative stress, membrane injury, osmotic stress, protein denaturation, as well as ion and nutrient imbalance, while exogenously applied or endogenously synthesized H₂S can alleviate these damages by enhancing the activity of antioxidant system, synthesizing osmolytes and heat shock proteins (HSPs) and regulating ion and nutrient balance (adapted from Min et al., 2016).

H₂S-Induced Salt Tolerance

Salts stress is negative effects of excessive salt on seed germination, plant growth and development, and even survival, which is a major abiotic stress in agriculture production worldwide. Salt stress commonly leads to direct and indirect injury, namely ion toxicity, osmotic stress, nutrient imbalance, and oxidative stress (Ahmad et al., 2013a,b). To combat with salt injury, plants have evolved many protective strategies, including osmotic adjustment by synthesizing osmolytes such as proline (Pro), glycine betaine (GB), trehalose (Tre), and total soluble sugar (TSS); ion and nutrient balance by regulating transporter; and enhancement of antioxidant capacity by activating the activity of antioxidant enzymes SOD, CAT, APX, GPX and glutathione reductase (GR), as well as by synthesizing antioxidants like AsA and GSH (Ahmad et al., 2013a,b). In salt-sensitive wheat cultivar LM15, the results of Bao et al. (2011) showed that wheat seed priming with different concentrations of NaHS (0.01, 0.05, 0.09, 0.13 mM) for 12 h could significantly alleviate the inhibition of seed germination and seedling growth induced by 100 mM NaCl in a concentration-dependent manner, as indicated in germination rate, germination index, vigor index and growth of seedlings of wheat. In alfalfa (*Medicago sativa*), NaHS pretreatment differentially activate total and isoenzymatic activities as well as corresponding transcripts of antioxidant enzymes (SOD, CAT, POD, and APX) under 100 mM NaCl stress, thus resulting in the alleviation of oxidative damage induced by NaCl (Wang et al., 2012). In addition, NaCl stress inhibited seed germination and seedling growth, but pretreatment with NaHS could significantly attenuate this inhibitive effect and increase the ratio of potassium (K) to sodium (Na) in the root parts (Wang et al., 2012). Also, under 100 mM NaCl stress, *Arabidopsis* roots displayed a great increase in electrolyte leakage and Na⁺/K⁺ ratio, indicating that *Arabidopsis* was sensitive to salt stress, while treatment with NaHS enhanced the salt tolerance by maintaining a higher K⁺/Na⁺ ratio (Li

J. et al., 2014). In addition, the level of gene expression and the phosphorylation of plasma membrane H⁺-ATPase and Na⁺/H⁺ antiporter protein was promoted by H₂S, while the effect of H₂S on the plasma membrane Na⁺/H⁺ antiporter system was removed by diphenylene iodonium (DPI, a PM NADPH oxidase inhibitor) or dimethylthiourea (DMTU, an ROS scavenger) (Li J. et al., 2014), suggesting that H₂S can maintain ion homeostasis in salt-stress *Arabidopsis* root in the H₂O₂-dependent manner.

H₂S-Induced Drought Tolerance

Similar to other stressors, drought stress, namely water deficiency, usually leads to osmotic stress and oxidative stress, which adversely affects plant growth, development and production (Iqbal et al., 2016). Plants can maintain water balance and ROS homeostasis by osmotic adjustment and antioxidant system (Foyer and Noctor, 2009, 2011; Iqbal et al., 2016). Zhang et al. (2010d) found that the germination rate reduced gradually with the increasing concentrations of PEG-6000, which mimicked osmotic stress, while NaHS treatment could promote wheat seed germination under osmotic stress in a dose-dependent manner, Na⁺ and other sulfur-containing components (S²⁻, SO₄²⁻, SO₃²⁻, HSO₄⁻, and HSO₃⁻) were not able to replace NaHS, confirming H₂S or HS⁻ derived from NaHS contribute to the protective roles (Zhang et al., 2010d). Further experiments showed that NaHS treatment significantly increased CAT and APX activities, reduced that of lipoxigenase as well as the accumulation of MDA and H₂O₂ in seeds (Zhang et al., 2010d). Additionally, exogenously applied NaHS increased the activities of APX, GR, dehydroascorbate reductase (DHAR) and gamma-glutamylcysteine synthetase in wheat seedlings, as well as the contents of AsA, GSH, total ascorbate and total glutathione under water stress compared to the control without NaHS treatment, which in turn decreased the MDA content and electrolyte leakage induced by water deficiency in wheat

seedlings (Shan et al., 2011). In *Arabidopsis* seedlings, under drought stress, the expression pattern of *L/DCD* was similar to the drought associated genes, whose expression was stimulated further by H₂S (Jin et al., 2011). Also, seedlings treated with NaHS exhibited a higher survival rate and a significant reduction in the size of the stomatal aperture compared to the control (Jin et al., 2011). In addition to these, García-Mata and Lamattina (2010) also found that, in *Vicia faba* (L.) var. major and *Impatiens walleriana* Hook. f., H₂S treatment could increase relative water content (RWC) and protect plants against drought stress.

H₂S-Induced Cold Tolerance

Low temperature stress includes chilling stress (>0°C) and freezing stress (<0°C). Low temperature usually leads to osmotic stress and oxidative stress, plants can reduce the low temperature injury by osmotic adjustment and activating antioxidant system (Foyer and Noctor, 2009, 2011; Iqbal et al., 2016). Shi et al. (2013) found that exogenous application of NaHS conferred multiple stress tolerance including freezing tolerances in bermudagrass, in reflected in decreased electrolyte leakage and increased survival rate under freezing conditions. Additionally, NaHS treatment mitigated the ROS burst and cell damage induced by freezing stress via modulating the activities of antioxidant enzymes CAT, GPX and GR, as well as non-enzymatic GSH pool and redox state (Shi et al., 2013). In grape (*Vitis vinifera* L) seedlings, Fu et al. (2013) reported that treatment with NaHS showed the high activity of SOD and gene expression of *VvICE1* and *VvCBF3*, lowered superoxide radical and MDA levels as well as cell membrane permeability under chilling stress at 4°C, while HT treatment displayed contrary effect under the chilling stress. Also, *Arabidopsis* seedlings overexpressing *LCD* or pretreating with NaHS exhibited higher endogenous H₂S level and stronger chilling stress tolerance, while *LCD* knockdown or HT pretreated plants displayed lower endogenous H₂S level and weaker stress resistance. Moreover, H₂S could up-regulate the expression of genes involved in multiple abiotic and biotic stress and inhibited ROS accumulation (Shi et al., 2015). Ma et al. (2015) found that the levels and enzyme activities of proteins involved in H₂S biosynthesis (*L/DCD*, *CAS*, *OAS-TL*) markedly increased at higher altitudes at 4800 and 5200 m, which in turn maintained higher H₂S level. Exogenous H₂S application reduced ROS and RNS (reactive nitrogen species) damage by increasing antioxidant enzyme and GSNOR (*S*-nitrosogluthathione reductase) activities, activated the downstream defense response, resulting in protein degradation as well as Pro and SS accumulation. However, such defense responses could be reversed by HT and PAG, respectively. These results illustrated that H₂S plays a central role in *L. rotata* uses multiple strategies to adapt to the alpine stress environment. Also, H₂S fumigation maintained higher values of lightness and peel firmness of banana fruit and reduced the accumulation of MDA under chilling stress (Luo et al., 2015). In addition, H₂S could increase the activities of GPX, SOD, CAT, APX, GR and the phenylalanine ammonia lyase and total phenolics content, which in turn improved antioxidant capacity of banana fruits, reducing H₂O₂ and superoxide anion accumulation (Luo et al., 2015). Further experiments also found

that H₂S fumigation elevated Pro content by activating P5CS activity and decreasing that of ProDH, which might be related to chilling injury tolerance improvement (Luo et al., 2015), similar to the report by Li and Gong (2013). These data indicate that H₂S alleviated the chilling injury may be achieved through the enhancement of antioxidant system and Pro accumulation in banana fruit.

H₂S-Induced Heat Tolerance

Along with global warming, high temperature has already become a noticeable abiotic stress worldwide, and the mechanisms of high temperature injury and heat tolerance have attracted much attention (Wahid et al., 2007; Asthir, 2015; Hemmati et al., 2015). Christou et al. (2011) found that pre-treatment of roots with NaHS effectively alleviated the decrease in leaf chlorophyll fluorescence, stomatal conductance and relative leaf water content in strawberry (*Fragaria x ananassa* cv. Camarosa) under heat stress at 42°C, as well as an increase in ion leakage and MDA accumulation in comparison with plants directly subjected to heat stress. In addition, NaHS pretreatment preserved AsA/GSH homeostasis, as evidenced by lower AsA and GSH pool redox disturbances and enhanced transcription of AsA and GSH biosynthetic enzymes, 8 h after heat stress exposure. Furthermore, NaHS root pretreatment increased the gene expression of antioxidant enzymes (*cAPX*, *CAT*, *MnSOD*, *GR*), heat shock proteins (*HSP70*, *HSP80*, *HSP90*), and aquaporins (*PIP*) (Christou et al., 2014). These results suggest that H₂S root pretreatment activates a coordinated network of heat shock defense-related pathways at a transcriptional level and systemically protects strawberry plants from heat stress-induced damage. Our previous study also showed that 0.7 mM NaHS treatment increased the activities of CAT, GPX, SOD and GR, and the contents of GSH and AsA, as well as the ratio of reduced antioxidants to total antioxidants [*AsA/(AsA+DHA)* and *GSH/(GSH +GSSG)*] in maize seedlings under normal culture conditions compared with the control (Li Z.G. et al., 2014). Under heat stress, antioxidant enzymes activities, antioxidants contents and the ratio of the reduced antioxidants to total antioxidants in control and treated seedlings all decreased, but NaHS-treated seedlings maintained higher antioxidant enzymes activities and antioxidants levels as well as reduced antioxidants/total antioxidants ratio (Li Z.G. et al., 2014), similar results also were found in tobacco cells (Li et al., 2015). In addition, NaHS pretreatment significantly increased the survival percentage of tobacco cells under heat stress and regrowth ability after heat stress, alleviated a decrease in vitality of cells and an increase in electrolyte leakage and MDA accumulation (Li et al., 2012b). Meanwhile, the heat tolerance induced by NaHS was markedly enhanced by exogenous application of Ca²⁺ and its ionophore A23187, respectively, while was weakened by addition of Ca²⁺ chelator ethylene glycol-bis(*b*-aminoethylether)-*N,N,N',N'*-tetraacetic acid, plasma membrane channel blocker La³⁺, as well as calmodulin antagonists chlorpromazine and trifluoperazine, respectively (Li et al., 2012b). Similarly, in maize, pretreatment with NaHS markedly improved the germination percentage of seeds and the survival percentage of seedlings under heat stress, alleviated an increase in electrolyte leakage

of roots and a decrease in tissue vitality and accumulation of MDA in coleoptiles of maize seedlings (Li et al., 2013a). Furthermore, NaHS pretreatment could improve the activity of Δ^1 -pyrroline-5-carboxylate synthetase (P5CS) and lowered that of Pro dehydrogenase (ProDH), which in turn induced the accumulation of endogenous Pro in maize seedlings (Li et al., 2013a). Also, exogenously applied Pro could increase endogenous Pro content, followed by increase in the survival percentage of maize seedlings under heat stress (Li et al., 2013a). These results suggest that NaHS pretreatment can improve the heat tolerance in plants and the acquisition of heat tolerance induced by NaHS may require the synergistic effect of antioxidant system, calcium messenger system, HSPs and Pro.

H₂S-Induced Flooding Tolerance and Pathogen Resistance

Flooding stress usually causes hypoxia, and even anoxia in plant roots, plants can improve hypoxia tolerance by reducing oxidative damage (van Dongen and Licausi, 2014). Cheng et al. (2013) found that hypoxia could induce root tip death of pea seedlings, while pretreatment with exogenous H₂S dramatically alleviated cell death by protecting root tip cell membranes from ROS damage induced by hypoxia and by inhibiting ethylene production. Conversely, root tip death induced by hypoxia was strongly enhanced by inhibiting the key enzymes responsible for endogenous H₂S biosynthesis (adding hydroxylamine to inhibit LCD activity). These results demonstrated that H₂S can enhance the tolerance of the plant to hypoxic stress by alleviating hypoxia-induced root tip death in pea seedlings.

More interestingly, H₂S also could transcriptionally regulate MIR393-mediate auxin signaling, including MIR393a/b and their target genes (TIR1, AFB1, AFB2, and AFB3), and this regulation was related with H₂S-induced antibacterial resistance (Shi et al., 2015).

All of the above studies in this section show exogenous application of NaHS (a H₂S donor) can induce cross-adaptation to HM, salt, osmosis, drought, cold, heat and hypoxia stresses in different plant species, and the optimal NaHS concentration range from 0.05 to 1.5 mM (Table 2), while higher NaHS concentration (>1.5 mM) exhibits negative effect on plant growth, development, survival, and even the acquisition of stress tolerance. Therefore, the optimal concentration of NaHS should be carefully selected according to plant species and experimental system.

CONCLUSION AND FUTURE PROSPECTIVE

In general, after undergoing a moderate stress, plants not only can improve the resistance to this stress, but also can increase the tolerance to subsequent other stresses, which known as cross-adaptation. Many studies found that signaling triggered by a moderate stress, such as Ca²⁺, ABA, H₂O₂, and NO signaling, is a common response of plants to abiotic and biotic stress, which

in turn induces the acquisition of cross-adaptation. In addition, exogenously applied these signal molecules also can trigger corresponding signaling, followed by improving stress tolerance of plants, thus Ca²⁺, ABA, H₂O₂, and NO are considered to be candidate signal molecules in cross-adaptation in plants (Knight, 2000; Gong et al., 2001; Li and Gong, 2011; Li et al., 2012b; Fang H. et al., 2014; Qiao et al., 2015; Chen et al., 2016). More recently, many research groups found that a number of abiotic stresses also can trigger H₂S signaling, while exogenously applied H₂S can induce cross-adaptation to multiple stresses, indicating that H₂S represents a potential candidate signal molecule in cross-adaptation in plants (Li, 2013; Lisjak et al., 2013; Calderwood and Kopriva, 2014; Hancock and Whiteman, 2014; Fotopoulos et al., 2015; Guo et al., 2016). However, H₂S acts as a signal molecule in plants cross-adaptation, the following questions need to be further answered: (1) Receptor or target of H₂S. Due to H₂S is easy to penetrate the cell membrane, maybe there is no H₂S receptor in plant cells, but Li et al. (2011) and Aroca et al. (2015) found that H₂S could modify the activity of some proteins with sulfhydryl (-SH) by sulfhydrylation (-SSH), whether these proteins are the receptors of H₂S needs to be further research. (2) Physiological concentration of H₂S. Many assay methods for H₂S including colorimetric, fluorescence-based, gas chromatographic and electrochemical methods give highly contrasting results (Table 2; Peng et al., 2012; Li, 2015b), so accurate physiological concentration of H₂S in plant cells or organelles is waiting for uncovering. It will be important to design the stress treatments closer to physiologically relevant stress intensities, thus low micromolar rather than millimolar HM concentration should be investigated in order to strengthen the conclusions. (3) Crosstalk between H₂S and other signal molecules in cross-adaptation. The acquisition of abiotic tolerance is involved in a signal network consisting of many signal molecules including H₂S, interaction among signal molecules needs to be updated and perfected. (4) Physiological, biochemical and molecular mechanisms of H₂S-induced cross-adaptation. The study on H₂S-induced abiotic tolerance including cross-adaptation has just started, many physiological, biochemical and molecular mechanisms require being expounded using transcriptome, proteome and metabolome approaches.

AUTHOR CONTRIBUTIONS

Z-GL wrote and revised the paper, XM and Z-HZ provided the idea.

ACKNOWLEDGMENTS

This research is supported by National Natural Science Foundation of China (31360057) and Doctor Startup Foundation of Yunnan Normal University China (01200205020503099). We appreciate the reviewers and editors for their exceptionally helpful comments about the manuscript.

REFERENCES

- Ahmad, P. (2016). *Plant Metal Interaction: Emerging Remediation Techniques*. Netherlands: Elsevier.
- Ahmad, P., Azooz, M. M., and Prasad, M. N. V. (2013a). *Ecophysiology and Responses of Plants under Salt Stress*. New York, NY: Springer.
- Ahmad, P., Azooz, M. M., and Prasad, M. N. V. (2013b). *Salt Stress in Plants: Signalling, Omics and Adaptations*. New York, NY: Springer.
- Aroca, A., Serna, A., Gotor, C., and Romero, L. C. (2015). S-sulphydration: a cysteine posttranslational modification in plant systems. *Plant Physiol.* 168, 334–342. doi: 10.1104/pp.15.00009
- Asthir, B. (2015). Mechanisms of heat tolerance in crop plants. *Biol. Plant.* 59, 620–628. doi: 10.1007/s10535-015-0539-5
- Bao, J., Ding, T. L., Jia, W. J., Wang, L. Y., and Wang, B. S. (2011). Effect of exogenous hydrogen sulfide on wheat seed germination under salt stress. *Modern Agric. Sci. Technol.* 20, 40–42.
- Bloem, E., Haneklaus, S., Kesselmeier, J., and Schnug, E. (2012). Sulfur fertilization and fungal infections affect the exchange of H₂S and COS from agricultural crops. *J. Agric. Food Chem.* 60, 7588–7596. doi: 10.1021/jf301912h
- Calderwood, A., and Kopriva, S. (2014). Hydrogen sulfide in plants: from dissipation of excess sulfur to signalling molecule. *Nitric Oxide* 41, 72–78. doi: 10.1016/j.niox.2014.02.005
- Chen, J., Wang, W. H., Wu, F. H., You, C. Y., Liu, W. T., Dong, X. K., et al. (2013). Hydrogen sulfide alleviates aluminum toxicity in barley seedlings. *Plant Soil* 362, 301–318. doi: 10.1007/s11044-012-1468-0
- Chen, X., Chen, Q., Zhang, X., Li, R., Jia, Y., Ef, A., et al. (2016). Hydrogen sulfide mediates nicotine biosynthesis in tobacco (*Nicotiana tabacum*) under high temperature conditions. *Plant Physiol. Biochem.* 104, 174–179. doi: 10.1016/j.plaphy.2016.02.033
- Cheng, W., Zhang, L., Jiao, C. J., Su, M., Yang, T., Zhou, L. N., et al. (2013). Hydrogen sulfide alleviates hypoxia-induced root tip death in *Pisum sativum*. *Plant Physiol. Biochem.* 70, 278–286. doi: 10.1016/j.plaphy.2013.05.042
- Christou, A., Filippou, P., Manganaris, G. A., and Fotopoulos, V. (2014). Sodium hydrosulfide induces systemic thermotolerance to strawberry plants through transcriptional regulation of heat shock proteins and aquaporin. *BMC Plant Biol.* 14:42. doi: 10.1186/1471-2229-14-42
- Christou, A., Manganaris, G., Papadopoulos, I., and Fotopoulos, V. (2011). “The Importance of hydrogen sulfide as a systemic priming agent in strawberry plants grown under key abiotic stress factors,” in *Proceedings of the 4th International Conference: Plant Abiotic Stress: From Systems Biology to Sustainable Agriculture*, Limassol, 47.
- Christou, A., Manganaris, G. A., Papadopoulos, I., and Fotopoulos, V. (2013). Hydrogen sulfide induces systemic tolerance to salinity and non-ionic osmotic stress in strawberry plants through modification of reactive species biosynthesis and transcriptional regulation of multiple defence pathways. *J. Exp. Bot.* 64, 1953–1966. doi: 10.1093/jxb/ert055
- Fang, H., Jing, T., Liu, Z., Zhang, L., Jin, Z., and Pei, Y. (2014). Hydrogen sulfide interacts with calcium signaling to enhance the chromium tolerance in *Setaria italica*. *Cell Calcium* 56, 472–481. doi: 10.1016/j.ceca.2014.10.004
- Fang, T., Cao, Z. Y., Li, J. L., Shen, W. B., and Huang, L. Q. (2014). Auxin-induced hydrogen sulfide generation is involved in lateral root formation in tomato. *Plant Physiol. Biochem.* 76, 44–51. doi: 10.1016/j.plaphy.2013.12.024
- Fotopoulos, V., Christou, A., Antoniou, C., and Manganaris, G. A. (2015). Hydrogen sulphide: a versatile tool for the regulation of growth and defence responses in horticultural crops. *J. Hortic. Sci. Biotechnol.* 90, 227–234.
- Foyer, C. H., and Noctor, G. (2009). Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. *Antioxid. Redox. Signal.* 11, 861–905. doi: 10.1089/ars.2008.2177
- Foyer, C. H., and Noctor, G. (2011). Ascorbate and glutathione: the heart of the redox hub. *Plant Physiol.* 155, 2–18. doi: 10.1104/pp.110.167569
- Foyer, C. H., Rasool, B., Davey, J. W., and Hancock, R. D. (2016). Cross-tolerance to biotic and abiotic stresses in plants: a focus on resistance to aphid infestation. *J. Exp. Bot.* 67, 2025–2037. doi: 10.1093/jxb/erw079
- Fu, P. N., Wang, W. J., Hou, L. X., and Liu, X. (2013). Hydrogen sulfide is involved in the chilling stress response in *Vitis vinifera* L. *Acta Soc. Bot. Pol.* 82, 295–302. doi: 10.5586/asbp.2013.031
- García-Mata, C., and Lamattina, L. (2010). Hydrogen sulphide, a novel gasotransmitter involved in guard cell signalling. *New Phytol.* 188, 977–984. doi: 10.1111/j.1469-8137.2010.03465.x
- Gong, M., Chen, B., Li, Z. G., and Guo, L. H. (2001). Heat-shock-induced cross adaptation to heat, chilling, drought and salt stress in maize seedlings and involvement of H₂O₂. *J. Plant Physiol.* 158, 1125–1130. doi: 10.1078/0176-1617-00327
- Gong, M., Li, Y. J., and Chen, S. Z. (1998a). Abscisic acid-induced thermotolerance in maize seedlings is mediated by calcium and associated with antioxidant systems. *J. Plant Physiol.* 153, 488–496. doi: 10.1016/S0176-1617(98)80179-X
- Gong, M., van der Luit, A. H., Knight, M. R., and Trewwas, A. J. (1998b). Heat-shock-induced changes in intracellular Ca²⁺ Level in tobacco seedlings in relation to thermotolerance. *Plant Physiol.* 116, 429–437. doi: 10.1104/pp.116.1.429
- Grover, M., Ali, S. Z., Sandhya, V., Rasul, A., and Venkateswarlu, B. (2011). Role of microorganisms in adaptation of agriculture crops to abiotic stresses. *World J. Microbiol. Biotechnol.* 27, 1231–1240. doi: 10.1007/s11274-010-0572-7
- Guo, H., Xiao, T., Zhou, H., Xie, Y., and Shen, W. (2016). Hydrogen sulfide: a versatile regulator of environmental stress in plants. *Acta Physiol. Plant.* 38:16. doi: 10.1007/s11738-015-2038-x
- Gupta, D. K., Corpas, F. J., and Palma, J. M. (2013). *Heavy Metal Stress in Plants*. Berlin: Springer.
- Hancock, J. T., and Whiteman, M. (2014). Hydrogen sulfide and cell signaling: team player or referee? *Plant Physiol. Biochem.* 78, 37–42. doi: 10.1016/j.plaphy.2014.02.012
- Hancock, J. T., and Whiteman, M. (2016). Hydrogen sulfide signaling: interactions with nitric oxide and reactive oxygen species. *Ann. N. Y. Acad. Sci.* 1365, 5–14. doi: 10.1111/nyas.12733
- Hemmati, H., Gupta, D., and Basu, C. (2015). “Molecular physiology of heat stress responses in plants,” in *Elucidation of Abiotic Stress Signaling in Plants: Functional Genomics Perspectives*, Vol. 2, ed. G. K. Pandey (New York, NY: Springer), 109–142.
- Hossain, M. A., Burrett, D. J., and Fujita, M. (2016). “Cross-stress tolerance in plants: molecular mechanisms and possible involvement of reactive oxygen species and methylglyoxal detoxification systems,” in *Abiotic Stress Response in Plants*, eds N. Tuteja and S. S. Gill (Chennai: Wiley), 323–375.
- Iqbal, N., Nazar, R., and Khan, N. A. (2016). *Osmolytes and Plants Acclimation to Changing Environment: Emerging Omics Technologies*. London: Springer.
- Jin, Z., and Pei, Y. (2015). Physiological implications of hydrogen sulfide in plants: pleasant exploration behind its unpleasant odour. *Oxid. Med. Cell Longev.* 2015, 1–6. doi: 10.1155/2015/758358
- Jin, Z., Shen, J., Qiao, Z., Yang, G., Wang, R., and Pei, Y. (2011). Hydrogen sulfide improves drought resistance in *Arabidopsis thaliana*. *Biochem. Biophys. Res. Commun.* 414, 481–486. doi: 10.1016/j.bbrc.2011.09.090
- Knight, H. (2000). Calcium signaling during abiotic stress in plants. *Int. Rev. Cytol.* 195, 269–324. doi: 10.1016/S0074-7696(08)62707-2
- Lai, D., Mao, Y., Zhou, H., Li, F., Wu, M., Zhang, J., et al. (2014). Endogenous hydrogen sulfide enhances salt tolerance by coupling the reestablishment of redox homeostasis and preventing salt-induced K⁺ loss in seedlings of *Medicago sativa*. *Plant Sci.* 225, 117–129. doi: 10.1016/j.plantsci.2014.06.006
- Li, J., Jia, H., Wang, J., Cao, Q., and Wen, Z. (2014). Hydrogen sulfide is involved in maintaining ion homeostasis via regulating plasma membrane Na⁺/H⁺ antiporter system in the hydrogen peroxide-dependent manner in salt-stress *Arabidopsis thaliana* root. *Protoplasma* 251, 899–912. doi: 10.1007/s00709-013-0592-x
- Li, L., Rose, P., and Moore, P. K. (2011). Hydrogen sulfide and cell signaling. *Annu. Rev. Pharmacol. Toxicol.* 51, 169–187. doi: 10.1146/annurev-pharmtox-010510-100505
- Li, Q., Wang, Z., Zhao, Y., Zhang, X., Zhang, S., Bo, L., et al. (2016). Putrescine protects hullless barley from damage due to UV-B stress via H₂S- and H₂O₂-mediated signaling pathways. *Plant Cell Rep.* 35, 1155–1168. doi: 10.1007/s00299-016-1952-8
- Li, Z. G. (2013). Hydrogen sulfide: a multifunctional gaseous molecule in plants. *Russ. J. Plant Physiol.* 60, 733–740. doi: 10.1134/S1021443713060058

- Li, Z. G. (2015a). Analysis of some enzymes activities of hydrogen sulfide metabolism in plants. *Methods Enzymol.* 555, 253–269. doi: 10.1016/bs.mie.2014.11.035
- Li, Z. G. (2015b). Quantification of hydrogen sulfide concentration using methylene blue and 5,5'-dithiobis (2-nitrobenzoic acid) methods in plants. *Methods Enzymol.* 554, 101–110. doi: 10.1016/bs.mie.2014.11.031
- Li, Z. G. (2015c). Synergistic effect of antioxidant system and osmolyte in hydrogen sulfide and salicylic acid crosstalk-induced heat tolerance in maize (*Zea mays* L.) seedlings. *Plant Signal. Behav.* 10:e1051278. doi: 10.1080/15592324.2015.1051278
- Li, Z. G., Ding, X. J., and Du, P. F. (2013a). Hydrogen sulfide donor sodium hydrosulfide-improved heat tolerance in maize and involvement of proline. *J. Plant Physiol.* 170, 741–747. doi: 10.1016/j.jplph.2012.12.018
- Li, Z. G., and Gong, M. (2011). Mechanical stimulation-induced cross-adaptation in plants: an overview. *J. Plant Biol.* 54, 358–364. doi: 10.1007/s12374-011-9178-3
- Li, Z. G., and Gong, M. (2013). Mechanical stimulation-induced chilling tolerance in tobacco (*Nicotiana tabacum* L.) suspension cultured cells and its relation to proline. *Russ. J. Plant Physiol.* 60, 149–154. doi: 10.1134/S1021443712060118
- Li, Z. G., Gong, M., and Liu, P. (2012a). Hydrogen sulfide is a mediator in H₂O₂-induced seed germination in *Jatropha curcas*. *Acta Physiol. Plant.* 34, 2207–2213. doi: 10.1007/s11738-012-1021-z
- Li, Z. G., Gong, M., Xie, H., Yang, L., and Li, J. (2012b). Hydrogen sulfide donor sodium hydrosulfide-induced heat tolerance in tobacco (*Nicotiana tabacum* L.) suspension cultured cells and involvement of Ca²⁺ and calmodulin. *Plant Sci.* 185–186, 185–189. doi: 10.1016/j.plantsci.2011.10.006
- Li, Z. G., and Gu, S. P. (2016). Hydrogen sulfide as a signal molecule in hematin-induced heat tolerance of tobacco cell suspension. *Biol. Plant.* 60, 595–600. doi: 10.1007/s10535-016-0612-8
- Li, Z. G., and He, Q. Q. (2015). Hydrogen peroxide might be a downstream signal molecule of hydrogen sulfide in seed germination of mung bean (*Vigna radiata*). *Biologia* 70, 753–759. doi: 10.1515/biolog-2015-0083
- Li, Z. G., and Jin, J.-Z. (2016). Hydrogen sulfide partly mediates abscisic acid-induced heat tolerance in tobacco (*Nicotiana tabacum* L.) suspension cultured cells. *Plant Cell Tiss. Organ. Cult.* 125, 207–214. doi: 10.1007/s11240-015-0939-4
- Li, Z. G., Long, W. B., Yang, S. Z., Wang, Y. C., Tang, J. H., Wen, L., et al. (2015). Endogenous hydrogen sulfide regulated by calcium is involved in thermotolerance in tobacco *Nicotiana tabacum* L. suspension cell cultures. *Acta Physiol. Plant.* 37:219. doi: 10.1007/s11738-015-1971-z
- Li, Z. G., Yang, S. Z., Long, W. B., Yang, G. X., and Shen, Z. Z. (2013b). Hydrogen sulfide may be a novel downstream signal molecule in nitric oxide-induced heat tolerance of maize (*Zea mays* L.) seedlings. *Plant Cell Environ.* 36, 1564–1572. doi: 10.1111/pce.12092
- Li, Z. G., Yi, X. Y., and Li, Y. T. (2014). Effect of pretreatment with hydrogen sulfide donor sodium hydrosulfide on heat tolerance in relation to antioxidant system in maize (*Zea mays*) seedlings. *Biologia* 69, 1001–1009. doi: 10.2478/s11756-014-0396-2
- Lin, Y. T., Li, M. Y., Cui, W. T., Lu, W., and Shen, W. B. (2012). Haem oxygenase-1 is involved in hydrogen sulfide-induced cucumber adventitious root formation. *J. Plant Growth Regul.* 31, 519–528. doi: 10.1007/s00344-012-9262-z
- Lisjak, M., Teklic, T., Wilson, I. D., Whiteman, M., and Hancock, J. T. (2013). Hydrogen sulfide: environmental factor or signalling molecule? *Plant Cell Environ.* 36, 1607–1616. doi: 10.1111/pce.12073
- Liu, X., Chen, J., Wang, G. H., Wang, W. H., Shen, Z. J., Luo, M. R., et al. (2016). Hydrogen sulfide alleviates zinc toxicity by reducing zinc uptake and regulating genes expression of antioxidative enzymes and metallothioneins in roots of the cadmium/zinc hyperaccumulator *L. Plant Soil* 400, 177–192. doi: 10.1007/s11104-015-2719-7
- Luo, Z., Li, D., Du, R., and Mou, W. (2015). Hydrogen sulfide alleviates chilling injury of banana fruit by enhanced antioxidant system and proline content. *Sci. Hortic.* 183, 144–151. doi: 10.1016/j.scienta.2014.12.021
- Ma, L., Yang, L., Zhao, J., Wei, J., Kong, X., Wang, C., et al. (2015). Comparative proteomic analysis reveals the role of hydrogen sulfide in the adaptation of the alpine plant *Lamiophlomis rotata* to altitude gradient in the Northern Tibetan Plateau. *Planta* 241, 887–906. doi: 10.1007/s00425-014-2209-9
- Min, X., Zhou, Z. H., and Li, Z. G. (2016). The metabolism of signal molecule hydrogen sulfide and its role in the acquisition of heat tolerance in plants. *Plant Physiol. J.* 52, 37–46.
- Mostofa, M. G., Rahman, A., Ansary, M. M. U., Watanabe, A., Fujita, M., and Tran, L. P. (2015). Hydrogen sulfide modulates cadmium-induced physiological and biochemical responses to alleviate cadmium toxicity in rice. *Sci. Rep.* 5:14078. doi: 10.1038/srep14078
- Niu, L., and Liao, W. (2016). Hydrogen peroxide signaling in plant development and abiotic responses: crosstalk with nitric oxide and calcium. *Front. Plant Sci.* 7:230. doi: 10.3389/fpls.2016.00230
- Pandey, G. K. (2015). *Elucidation of Abiotic Stress Signaling in Plants: Functional Genomics Perspectives*. New York, NY: Springer.
- Peng, H. J., Chen, W. X., and Wang, B. H. (2012). “Methods for the detection of gasotransmitters,” in *Gasotransmitters: Physiology and Pathophysiology*, eds A. Hermann, G. F. Sitdikova, and T. M. Weiger (Heidelberg: Springer), 99–137.
- Pineda, A., Pangesti, N., Soler, R., van Dam, N. M., van Loon, J. J. A., and Dicke, M. (2016). Negative impact of drought stress on a generalist leaf chewer and a phloem feeder is associated with, but not explained by an increase in herbivore-induced glucosinolates. *Environ. Exp. Bot.* 123, 88–97. doi: 10.1016/j.envexpbot.2015.11.007
- Qiao, Z., Jing, T., Liu, Z., Zhang, L., Jin, Z., Liu, D., et al. (2015). H₂S acting as a downstream signaling molecule of SA regulates Cd tolerance in *Arabidopsis*. *Plant Soil* 393, 137–146. doi: 10.1007/s11104-015-2475-8
- Scuffi, D., Lamattina, L., and García-Mata, C. (2016). Gasotransmitters and stomatal closure: is there redundancy, concerted action, or both? *Front. Plant Sci.* 7, 277. doi: 10.3389/fpls.2016.00277
- Shan, C. J., Zhang, S. L., Li, D. F., Zhao, Y. Z., Tian, X. L., Zhao, X. L., et al. (2011). Effects of exogenous hydrogen sulfide on the ascorbate and glutathione metabolism in wheat seedlings leaves under water stress. *Acta Physiol. Plant.* 33, 2533–2540. doi: 10.1007/s11738-011-0746-4
- Shen, J., Xing, T., Yuan, H., Liu, Z., Jin, Z., Liu, Z., et al. (2013). Hydrogen sulfide improves drought tolerance in *Arabidopsis thaliana* by microRNA expressions. *PLoS ONE* 8:e77047. doi: 10.1371/journal.pone.0077047
- Shi, H., Ye, T., and Chan, Z. (2013). Exogenous application of hydrogen sulfide donor sodium hydrosulfide enhanced multiple abiotic stress tolerance in bermudagrass (*Cynodon dactylon* (L.) Pers.). *Plant Physiol. Biochem.* 71, 226–234. doi: 10.1016/j.plaphy.2013.07.021
- Shi, H., Ye, T., Han, N., Bian, H., Liu, X., and Chan, Z. (2015). Hydrogen sulfide regulates abiotic stress tolerance and biotic stress resistance in *Arabidopsis*. *J. Integr. Plant Biol.* 57, 628–640. doi: 10.1111/jipb.12302
- Singh, V. P., Singh, S., Kumar, J., and Prasad, S. M. (2015). Hydrogen sulfide alleviates toxic effects of arsenate in pea seedlings through up-regulation of the ascorbate–glutathione cycle: possible involvement of nitric oxide. *J. Plant Physiol.* 181, 20–29. doi: 10.1016/j.jplph.2015.03.015
- van Dongen, J. T., and Licausi, F. (2014). *Low-Oxygen Stress in Plants: Oxygen Sensing and Adaptive Responses to Hypoxia*. Wien: Springer.
- Wahid, A., Gelani, S., Ashraf, M., and Foolad, M. R. (2007). Heat tolerance in plants: an overview. *Environ. Exp. Bot.* 61, 199–223. doi: 10.1016/j.envexpbot.2007.05.011
- Wang, L., Wan, R., Shi, Y., and Xue, S. (2016). Hydrogen sulfide activates S-type anion channel via OST1 and Ca²⁺ modules. *Mol. Plant* 9, 489–491. doi: 10.1016/j.molp.2015.11.010
- Wang, R. (2012). Physiological implications of hydrogen sulfide: a whiff exploration that blossomed. *Physiol. Rev.* 92, 791–896. doi: 10.1152/physrev.00017.2011
- Wang, Y. Q., Li, L., Cui, W. T., Xu, S., Shen, W. B., and Wang, R. (2012). Hydrogen sulfide enhances alfalfa (*Medicago sativa*) tolerance against salinity during seed germination by nitric oxide pathway. *Plant Soil* 351, 107–119. doi: 10.1007/s11104-011-0936-2
- Wojtyła, L., Lechowska, K., Kubala, S., and Garnczarska, M. (2016). Different modes of hydrogen peroxide action during seed germination. *Front. Plant Sci.* 7:66. doi: 10.3389/fpls.2016.00066
- Yadav, S. K. (2010). Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatin in heavy metal stress tolerance of plants. *S. Afr. J. Bot.* 76, 167–179. doi: 10.1016/j.sajb.2009.10.007
- Yamasaki, H., and Cohen, M. F. (2016). Biological consilience of hydrogen sulfide and nitric oxide in plants: gases of primordial earth linking plant, microbial and animal physiologies. *Nitric Oxide* 5, 91–100. doi: 10.1016/j.niox.2016.04.002
- Zhang, H., Dou, W., Jiang, C. X., Wei, Z. J., Liu, J., and Jones, R. L. (2010a). Hydrogen sulfide stimulates β-amylase activity during early stages of wheat grain germination. *Plant Signal. Behav.* 5, 1031–1033. doi: 10.4161/psb.5.8.12297

- Zhang, H., Hu, L. Y., Li, P., Hu, K. D., Jiang, C. X., and Luo, J. P. (2010b). Hydrogen sulfide alleviated chromium toxicity in wheat. *Biol. Plant.* 54, 743–747. doi: 10.1007/s10535-010-0133-9
- Zhang, H., Hu, L. Y., Hu, K. D., He, Y. D., Wang, S. H., and Luo, J. P. (2008). Hydrogen sulfide promotes wheat seed germination and alleviates oxidative damage against copper stress. *J. Integr. Plant Biol.* 50, 1518–1529. doi: 10.1111/j.1744-7909.2008.00769.x
- Zhang, H., Hu, S. L., Zhang, Z. J., Hu, L. Y., Jiang, C. X., Wei, Z. J., et al. (2011). Hydrogen sulfide acts as a regulator of flower senescence in plants. *Postharv. Biol. Technol.* 60, 251–257. doi: 10.1016/j.postharvbio.2011.01.006
- Zhang, H., Tan, Z. Q., Hu, L. Y., Wang, S. H., Luo, J. P., and Jones, R. L. (2010c). Hydrogen sulfide alleviates aluminum toxicity in germinating wheat seedlings. *J. Integr. Plant Biol.* 52, 556–567. doi: 10.1111/j.1744-7909.2010.00946.x
- Zhang, H., Wang, M. F., Hua, L. Y., Wang, S. H., Hua, K. D., Bao, L. J., et al. (2010d). Hydrogen sulfide promotes wheat seed germination under osmotic stress. *Russ. J. Plant Physiol.* 57, 532–539. doi: 10.1134/S1021443710040114
- Zhang, L., Pei, Y., Wang, H., Jin, Z., Liu, Z., Qiao, Z., et al. (2015). Hydrogen sulfide alleviates cadmium-induced cell death through restraining ROS accumulation in roots of *Brassica rapa* L. ssp. *pekinensis*. *Oxid. Med. Cell Longev.* 2015, 1–11. doi: 10.1155/2015/714756

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer SM and handling Editor declared their shared affiliation, and the handling Editor states that the process nevertheless met the standards of a fair and objective review.

Copyright © 2016 Li, Min and Zhou. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.