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Hydrogen Sulfide: A Novel Gaseous Molecule for Plant Adaptation to Stress

Mukhtar Ahmed[1,2] · Shah Fahad[3,4] · Muhammad Arif Ali[5] · Sajjad Hussain[6] · Muhammad Tariq[7,8] · Fariha Ilyas[5] · Shakeel Ahmad[7] · Shah Saud[9] · Hafiz Mohkum Hammad[10] · Wajid Nasim[11] · Chao Wu[12] · Hongyan Liu[3]

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Abstract

Hydrogen sulfide (H_2S) has emerged as a novel gaseous signal molecule with multifarious effects on seed germination, plant growth, development, and physiological processes. Due to its dominant role in plant stress tolerance and cross-adaptation, it is getting more attention nowadays, although it has been largely referred as toxic and environmental hazardous gas. In this review work, we are highlighting the importance of H_2S as an essential gaseous molecule to help in signaling, metabolism, and stress tolerance in plants. Firstly, production of H_2S from different natural and artificial sources were discussed with its transformation from sulfur (S) to sulfate (SO_4^{2-}) and then to sulfite (SO_3^{2-}). The importance of different kinds of transporters that helps to take SO_4^{2-} from the soil solution was presented. Mainly, these transporters are SULTRs (H^+/SO_4^{2-} cotransporters) and multigene family encodes them. Furthermore, these SULTRs have LAST (Low affinity transport proteins), HAST (High affinity transport proteins), vacuole transporters, and plastid transporters. Since it is well known that there is strong relationship between SO_4^{2-} and synthesis of hydrogen sulfide or dihydrogen sulfide or sulfane in plant cells. Thus, cysteine (Cys) metabolism through which H_2S could be generated in plant cell with the role of different enzymes has been presented. Furthermore, H_2S in interaction with other molecules could help to mitigate biotic and abiotic stress. Based on this review work, it can be concluded that H_2S has potential to induce cross-adaptation to biotic and abiotic stress; thus, it is recommended that it should be considered in future studies to answer the questions like what are the receptors of H_2S in plant cell, where in plants the physiological concentration of H_2S is high in response to multiple stress and how it induces cross-adaptation by interaction with other signal molecules.

Keywords Hydrogen sulfide · Physiological processes · Abiotic stress · Natural and artificial sources · Molecular mechanism

Abbreviations

ABA	Abscisic acid
CAS	Cyano alanine synthase
CS	Cysteine synthase
Cys	Cysteine
DES1	L-Cysteine Desulhydrase
DMS	Dimethyl sulfide
HAST	High affinity transport proteins
LAST	Low affinity transport proteins
LCDSH/DCDSH	L- and D-cysteine desulfhydrase
MAPK	Mitogen-activated protein kinase
PTMs	Persulfidation and S-nitrosation
SR	Sulfite reductase

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✉ Shah Fahad
shahfahad@uoswabi.edu.pk

Extended author information available on the last page of the article

Introduction

Hydrogen sulfide (H_2S) is a colorless, low molecular weight, and soluble gas which had been known for its bad odor and phytotoxic effects for centuries. It is present in atmosphere and mainly added through volcanos, salt marshes, wet land, geothermal vents, livestock, industry, combustion of biomass and fossil fuels, and bacterial anaerobic respiration. Hydrogen sulfide represents only 8.5% (i.e., 4.4 Tg) of the total annual natural sulfur emission (i.e., 52 Tg) (Watts 2000). The H_2S is present in the atmosphere and plants may take it through foliage which negatively affects the normal sulfate metabolism in plants that is uptaken by plant roots

(Ausma and Kok 2019). The H_2S is absorbed through foliage via stomata and acts as substantial nutrient source of sulfur (S) in plants. For S homeostasis in plants, these must have to maintain the ability to emit it temporarily through foliage to atmosphere (Schröder 1993). The detoxification and removal of H_2S from plants is more important when H_2S is just a pollutant. In such circumstances, the role of H_2S is not just a signaling molecule (Lisjak et al. 2013).

Most studies about H_2S focused on animals, while studies on the effect of H_2S on plants only started to be more frequent during the late part of the twentieth century (Wang 2002). Its endogenous generation in plants as signaling molecule and its direct and indirect role in stress tolerance and protection against diseases was realized after 1975, time until which it was only considered as a determinant of plant growth and development. At that time, results reported by Joshi et al. (1975) indicated that H_2S inhibits the oxygen release from rice seedlings and nutrient uptake. A few years later, results about the impact of H_2S fumigation on forest plant were published (Thompson and Kats 1978a, b).

Reported negative impacts of H_2S include respiration inhibition in hemp (Martin and Maricle 2015), decrease in freezing tolerance of wheat (Stuiver et al. 1992), inhibition of photoreduction of $NADP^+$ in spinach (De Kok et al. 1983), and inhibition of activity of cytochrome oxidase in the mitochondria (Dorman et al. 2002). However, the impact of H_2S on plants are dose specific and low doses may rather be beneficial for crop growth and development (Dooley et al. 2013; Filipovic and Jovanović 2017). However, plants species vary greatly to atmospheric H_2S phytotoxicity, revealing that various doses have differential effects on plants. These are mainly attributed due to differences in leave absorption capacity, leaf elongation rate, and other related physiological and morphological traits. Plants with tolerance to atmospheric H_2S could be utilized in regions characterized as highly pollutant with H_2S.

Most of the studies carried out on investigation of H_2S on growth and physiological parameters were carried out with Sodium hydrosulfide (NaHS) as a donor of H_2S. However, sodium sulfide (Na_2S) has also been described as important H_2S donor (Ziogas et al. 2018). The NaHS rapidly dissociated to generate H_2S and hence used in most of studies to evaluate the H_2S impacts on plants. The GYY4137 (morpholin4-ium 4 methoxyphenyl(morpholino) phosphinodithionate may be another donor of H_2S (Lisjak et al. 2010). Nutritionally, it is important with respect to sulfur source, a major nutrient and component of s-containing amino acid such as cysteine and methionine.

Hydrogen sulfide acts as signaling molecules in stress along with interplay with other plant hormones, signaling molecules, and reactive oxygen species. Globally, now it is being applied for protection against stresses including drought (Ma et al. 2016a, b), waterlogging (Xiao et al. 2020), heavy metals (Thapa et al. 2012), salinity (Christou et al. 2011), inhibition of autophagy (Filipovic and Jovanović 2017), and fruit ripening (Ziogas et al. 2018). Some of the benefits associated with the use of H_2S include enhancement in processes like seed germination, root proliferation, stomatal closure, leaf senescence, maintenance of K^+/Na^+ balance, and improvement in fruit shelf life and quality. Table 1 described the dose of NaHS application which is most important for exogenous application. Due its lipophilic and gaseous nature, H_2S can be easily transported through cell membrane and within plant bodies. The waterlogged conditions create hypoxia stress and root respiration is primarily suffered oxygen deficiency in such conditions. The H_2S application played a protective role against oxidative damages imposed by waterlogged conditions through reducing accumulation of reactive oxygen species in roots and leaves of peach (Xiao et al. 2020). It triggers the gene expression in grapevine related to biosynthesis of metabolites which are used to improve production of defensive compounds (Ma and Yang 2018). Moreover, evidence from tomato concluded that H_2S application from NaHS regulated the expression of more five thousand genes (Guo et al. 2018). The H_2S as stress tolerance molecules sustain crop growth and development through regulating the production of reactive oxygen species. Application of H_2S may also increase the level of various antioxidant components, resulting in an improved tolerance (Corpas and Palma 2020). Keeping in view the important regulatory role in management of abiotic

Table 1 Description of alleviating impacts of various stresses through H_2S application

Crop name	Donor's name	Conc. of donor	Impacts	References
Strawberry	NaHS	0.8 mM	Improving post-harvest life of fruit and reducing rottening	Hu et al. (2012)
Banana	NaHS	1.0 mM	Alleviate the impact of ethylene production and reduce fruit softening	Ge et al. (2017)
Avacado	NaHS	200 µmM	Protection against frost and day light	Joshi et al. (2020)
Rice	NaHS	2 µM	Reduce aluminum in roots, reduce H_2O_2 levels	Zhu et al. (2018)
Maize	NaHS	500 µM	Reduce chromium toxicity and improve antioxident activity	Kharbech et al. (2017)
Wheat	NaHS	50 µM	Reduce ROS	Deng et al. (2016)
Cotton	NaHS	200 µM	Improved plant growth, photosynthesis, relieved Pb stress	Bharwana et al. (2014a,b)

and biotic stress, it is now being applied exogenously for additional protection.

The post-harvest deterioration of fruit quality is an important issue of producers, marketing agents, and consumers. Exogenously applied H_2S may impact the fruit ripening process and post-harvest quality, by reducing the activity of enzymes like superoxide dismutase, catalase, peroxidase, and other related enzymes for reducing the levels of reactive oxygen species. It is helpful to preserve vitamin C, soluble protein, and total phenols along with other fruit quality traits in apple and grapes (Zheng et al. 2016; Ni et al. 2016). The anti-ripening role of H_2S results from the interplay with ethylene in fruits (Ge et al. 2017). The regulation of H_2S concentration during transition of ripening stages was also reported in sweet pepper (Muñoz-Vargas et al. 2018). The current review mainly focused on H_2S application in the field of agriculture in term of stress tolerance molecule, growth promotion, and preservation of post-harvest quality. The main objective of this review is to highlight the biosynthesis, sources, absorption, translocation, and regulatory role of H_2S in stress tolerance for exogenous applications in field conditions for dealing various issues of crop production.

Artificial and Natural Sources of H_2S for Plant Cells

To be effective in plant cells, H_2S gas must be present in high concentration. There are two sources of H_2S emission in environment, i.e., anthropogenic and natural source. Among anthropogenic activities, the main source of H_2S emission is from combustion of fuels. Other manmade sources include geothermal industries, wastewater treatment, and agriculture activities. Areas located near geothermal site faced 50 ppb H_2S. Modern cars that have catalytic inverters also emit H_2S gas (Kourtidis et al. 2008). Drilling and refining, coke oven, paper making process and waste treatment processes emit H_2S gas in sufficient amount. In mining process, during the decomposition of xanthates in presence of water also produce H_2S (Bhomick and Rao 2014).

Natural gas is considered a more environment friendly fuel as it emits about 50% less carbon dioxide in atmosphere as compared to coal. Increasing demand of natural gas leads to the depletion of natural reservoirs, and trend is shifting toward the use of gas extracted from undesirable lands, such as shale gas reservoirs (Goodwin et al. 2015; Brace and Engelberth 2020). Natural gas obtained from such reservoirs is highly acidic and concentrated with H_2S gas and considered as sour gas. In 2004, sour gas contributed 21% among total natural gas and predicted to be 27% in 2030, which will be a major health concern in future (Goodwin et al. 2015).

Volcanoes are considered to be major natural source of H_2S gas emission (Aiuppa et al. 2005). Plants grown in such regions would be resistant from H_2S. It is also released from marshlands, anoxic soils, ground water, and coastal sediments (Hansen et al. 1978). Areas near coastal regions face 5–30 μg/m^3 H_2S concentration in atmosphere (Kourtidis et al. 2008).

Sulfur Dynamics and Synthesis of H_2S in Soil

Besides volcanoes, other natural sources of H_2S include coastal marine sediments and anoxic soils of marshland. Archaea (e.g., *Archaeoglobus*) and Bacteria (e.g., *Desulfovibrio*, *Desulfobacter*) present in waterlogged soils and marshy places produce sulfur (S)-based compounds such as sulfate (SO_4^{2-}) which is then transformed into sulfite (SO_3^{2-}). According to the genesis point of view, H_2S mainly comes from the four sources i.e., volcanic inorganic sources, SO_4^{2-} reduction by bacteria (SRB), decomposition of organic S compounds by heat, and SO_4^{2-} reduction by the thermochemical reactions (Ma et al. 2019).

Production of H_2S in waterlogged soils is mainly due to the reduction of SO_4^{2-}. The reduction that occurs only in these soils is due to the presence of anaerobic bacteria. This is also a major reaction of S cycling that prevails in waterlogged soils due to the readily decomposition of plant residues e.g., alfalfa (*Medicago sativa*). The SO_4^{2-} reduction due to bacteria involves assimilation (SO_4^{2-} is reduced to the thiol) or dissimilation (SO_4^{2-} reduction leads to the production of H_2S) processes. Since soil is main source of H_2S production, it is essential to report about availability of S in the earth crust, which is the main reagent for the synthesis of H_2S. The average S content of the earth crust is in the range of 0.06 to 0.10% and it is ranked as 13th most abundant element in nature (Tabatabai 2005). Minerals of S are available in rocks and soils as SO_4^{2-} (e.g., Epsomaite ($MgSO_4.7H_2O$), Mirabilite ($Na_2SO_4.10H_2O$), Gypsum ($CaSO_4.2H_2O$), Gypsum anhydorous ($CaSO_4$)), and as S^{-2} (e.g., Arseno pyrite ($FeS_2.FeAs_2$), chalcopyrite ($CuFeS_2$), cobaltite (CoAsS), galena (PbS), marcasite (FeS_2), pentlandite $(Fe, Ni)_9S_8$, pyrrhotite ($Fe_{11}S_{12}$) sphalerite (ZnS)). There is continuous flow of S going on between terrestrial and marine masses (Fuentes-Lara et al. 2019). The simple biogeochemical cycle that shows transformation of S to different forms is shown in Fig. 1.

Generally, two types of S occur in soil i.e., Organic and inorganic. Organic S in soil accounts for 95% of the total S in the humid and semi humid regions. The S availability to the plants in agricultural ecosystems follows different mechanisms as shown in Fig. 2. From atmosphere, it comes from aerosols of S and S gaseous forms as well as dissolved S (SO_4^{2-}) in snow and rain. Similarly, oxidation of S from soil organic matter and S^o also generates SO_4^{2-}. These SO_4^{2-} can be leached to the subsoil or fixed in the soil exchange matrix

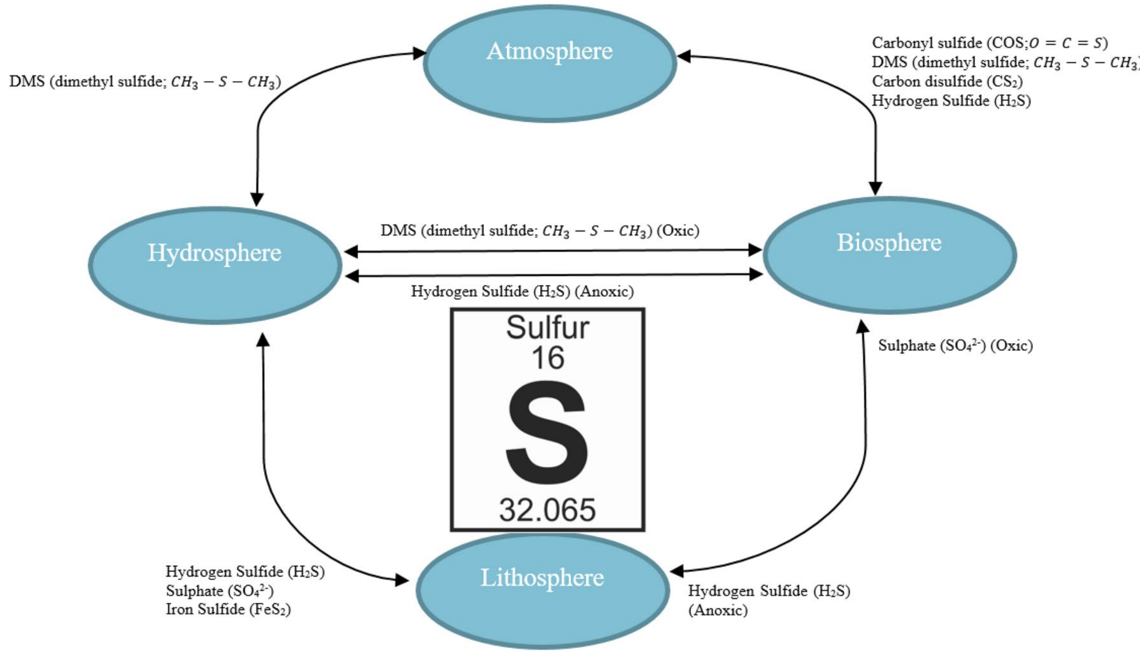


Fig. 1 Biogeochemical S cycle between different spheres

(Chao et al. 1962). Large quantities of SO_4^{2-} in the subsoil of arid regions are also available as gypsum ($CaSO_4$), while in the regions where rainfall is high this SO_4^{2-} leached down to the lower horizons (Johnson and Cole 1980).

The SO_4^{2-} in the soil is subjected to two kind of reactions i.e., dissimilatory (SO_4^{2-} acts as final acceptor of electrons in the anaerobic metabolisms of microbes producing H_2S that on re-oxidation goes to the atmosphere) and assimilatory reduction (Biosynthesis of organic compounds through algae, fungi, plants and prokaryotes e.g., amino acids). Assimilatory reduction of SO_4^{2-} is not possible by animals and protists; thus, they depend on other organism that synthesizes the organic S compounds (Andreae 1990). The dissimilatory reduction of SO_4^{2-} results in the production of S^0 mostly under anoxic conditions. This S^0 could be assimilated into S^{2-} that will be part of the biomolecules or volatilized in the case of excess S (Fig. 2). Plant can be a source or sink of volatile forms of S such as H_2S, DMS (dimethyl sulfide; $CH_3 - S - CH_3$), carbon disulfide (CS_2) etc.

Availability of S for many crop species is very beneficial as it improves the nutritional quality as well as tolerance to the biotic and abiotic stresses (Tea et al. 2004; González-Morales et al. 2017; Corpas et al. 2020; Fuentes-Lara et al. 2019; Corpas and Palma 2020; Nawaz et al. 2020; Zhang and Liao 2020). Tabatabai (2005) reported significant relationship of Sulfur with Carbon (C), Nitrogen (N), and Phosphorus (P) in soils around the globe. However, S availability as inorganic form like N is very small as compared to the organic forms, but P is abundantly available in both forms. Thus, relationship between total N, organic P, organic C, and total S has been reported mostly. The mean C: N: P: S ratios for the agricultural soil is 130:10:1.3:1.3, while for the peat and organic soils it is 160:10:1.2:1.2 and the soil under native grass has ratio of 200:10:1:1.

Absorption and Translocation

The absorption of S in plant cell is mostly in the form of H_2S, DMS, COS, and SO_2. However, most of the S is taken up by the plants from the soil solution as SO_4^{2-} (Wainwright 1984; Rennenberg 1989). Different kinds of transporters help to take SO_4^{2-} from the soil solution. Mainly, these transporters are SULTRs (H^+/ SO_4^{2-} cotransporters) and multigene family encodes them. Furthermore, these SULTRs have LAST (Low affinity transport proteins), HAST (High affinity transport proteins), vacuole transporters and plastid transporters (Fig. 3). The concentration of SO_4^{2-} that induces HAST is less than 10 mg dm^{-3} (Fuentes-Lara et al. 2019). Absorption of SO_4^{2-} in the root is facilitated by HAST, SULTR 1:1, SULTR 1:2, and SULTR 1:3 in the presence of ATPase enzyme as shown in Fig. 3. In the epidermis and cortex of root HAST are present abundantly, while in the parenchyma cell adjacent to the vascular bundles (Xylem and phloem) LAST dominates.

The cotransporters SULTR 4:1 and 4:2 help the vacuoles to absorb SO_4^{2-} which is then stored there. This can be further redistributed to different plant parts depending upon the demand. Xylem and phloem helps to transport and translocate SO_4^{2-} from the roots to stems

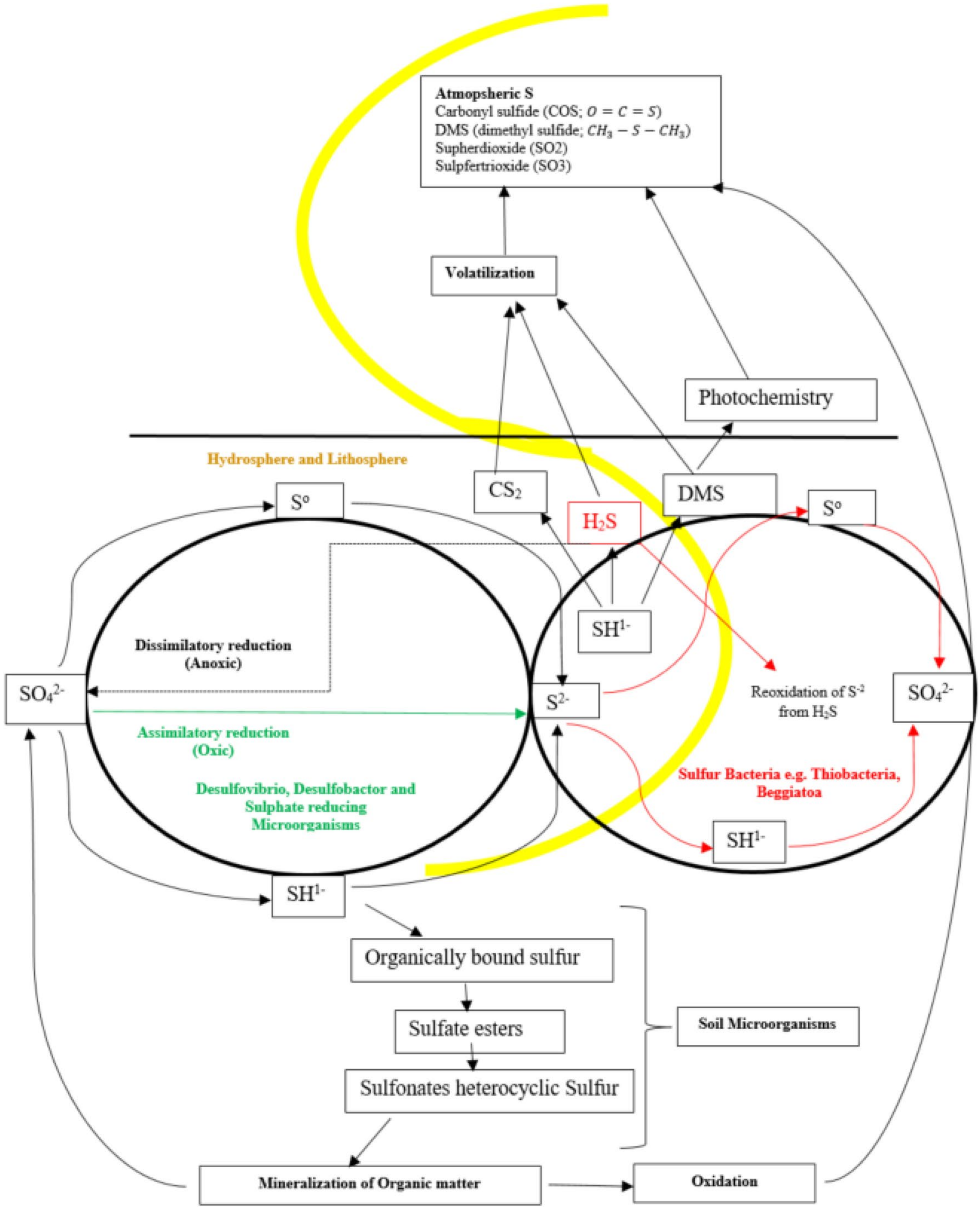


Fig. 2 S availability mechanisms to plants in agricultural ecosystems

and afterward to the leaves and seeds through different kinds of SULTRs (Yoshimoto et al. 2003; Kataoka et al. 2004; Takahashi et al. 2011; Cao et al. 2013; Maruyama-Nakashita 2017; Kirschner et al. 2018; Singh and Schwan 2019). The absorbed SO_4^{2-} is largely assimilated into proteins and other biomolecules, while in some plants e.g., *Brassica* spp., it might be present in the plant tissues. The SO_4^{2-} absorbed by the xylem is discharged in the mesophyll cell of the leaf with the help of HAST and LAST. Some of this SO_4^{2-} is stored in the vacuoles, while other moves to the chloroplast through SULTR3:1, SULTR3:2, SULTR 3:3, and SULTR 3:4, where it is reduced to S^{2-} and assimilated to the biological molecules. The stored sulfate can be remobilized through the

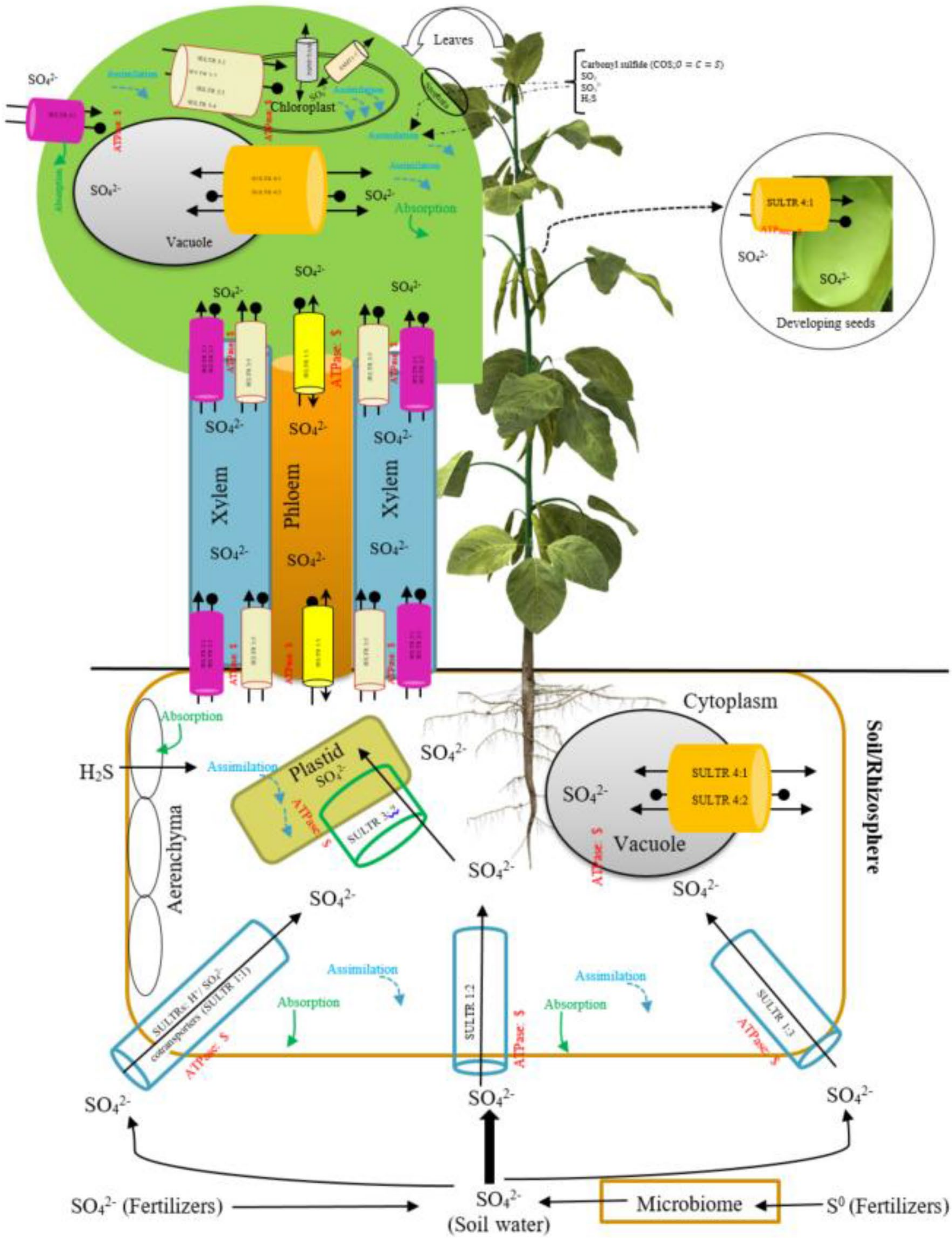


Fig. 3 Sulfate (SO_4^{2-}) uptake from soil solution to different plant parts and role of SULTRs (H^+/ SO_4^{2-} cotransporters)

SULTR 4:1 and SULTR 4:2 (Fig. 3). Excessive accumulation of SO_4^{2-} is possible if excess of S is available which further leads to the formation of volatile compounds e.g., H_2S (Rennenberg 1989). Since H_2S is a weak acid, it can be changed to different form as shown in the following equation:

$$H_2S \leftrightarrow H_2S_{Aquoesossolution} \leftrightarrow HS^- + H^+ \leftrightarrow S^{2-} + 2H^+$$

Detrimental Effects of Hydrogen Sulfide

Hydrogen sulfide has been considered as a phytotoxin since long time, for its deleterious effects on plant growth (Lisjak et al. 2013). It is lipophilic in nature and can easily cross the cell membrane and its effects on the two important PTMs processes (persulfidation and S-nitrosation) by reaction with Cys-protein thiol group. These proteins regulate the productivity of redox species and signaling (Spadaro et al. 2010). Oxidation state of S varies from − 2 (thiol) to + 4 (sulfonic acid) and its variation further depends upon ROS contents.

In 1975, it was first identified that at toxic level, H_2S gas is detrimental for plant health. Joshi et al. (1975) reported inhibited O_2 release from six rice cultivar seedlings, when exposed to H_2S. In few cultivars, it also negatively affected on plant nutritional status especially phosphorous nutrition. Continuous fumigation of H_2S at 3000 ppb on *Medicago*, sugar beet, pine, lettuce, and grapes caused leaf lesions leading to defoliation (Thompson and Kats 1978a, b). Defoliation is caused by mutation in two T-DNA, *des1-1* and *des 1–2* of *Arabidopsis thaliana* plants. Enzymes responsible for production of H_2S in plants is L-cysteine desulfhydrase, and increased activity of this enzyme alters the gene expression and transcription factor which are associated with the leaf senescence due to increased cysteine concentration in plant leaf (Alvarez et al. 2010).

Furthermore, studies also reported the cross talk between H_2S and NO, which is toxic at higher concentration (Wang 2003). H_2S promotes the production of NO which controls the stomatal closure process by regulating the abscisic acid concentration (Jin et al. 2013). Increased H_2S concentration in plant tissues also reduced the auxin translocation and synthesis followed by modulation in PIN proteins distribution resulting in restricted root growth (Jia et al. 2015). The cytochrome oxidase is an crucial enzyme in mitochondrial respiration which is involved in electron transport chain. The inhibition of cytochrome oxidase activity due to H_2S had been recognized in experiments conducted for rice (Xiao et al. 2010).

Role of H_2S Systems in Morpho-Physiological Processes

In recent years, H_2S started to be considered as a signaling molecule in various physiological functions. It is now considered as third gaseous signaling molecule after CO_2 and NO. From seed germination to maturity, it is thought to be involved in various physiological functions in aerobic and anaerobic organisms (Corpas and Palma 2020). In studies, a very narrow concentration of H_2S application to plants showed positive response which showed that H_2S acts as signaling molecule in plants (Joshi et al. 2020; Zhang et al. 2020). It actively takes part in various physiological processes like photosynthesis, defense and growth metabolism. Studies reported that it increases plant tolerance from heat, heavy metal stress, and nutrient stress by increasing photosynthesis rate via increasing ribulose-1, 5-bisphosphate carboxylase activity (Chen et al. 2011; Arnao and Hernandez-Ruiz 2015). It also improves stomatal density which further affects positively the photosynthesis rate. Seedlings treated with 0.01 mM H_2S reduce photorespiration and increase stomatal density which leads to high photosynthesis activity. Photorespiration is reduced due to the downregulation of *Glycolate oxidase*, enzyme involved in C_2 cycle in photorespiration (Duan et al. 2015).

Studies showed that H_2S provides S to protein thiol group (-SH) and produces persulphide group (-SSH). This played a vital role in modulating the responses of selected proteins (Aroca et al. 2018). NaHS application, which is a donor of H_2S improves seed germination rate by upregulating β-amylase activity in endosperm and downregulating the MDA and H_2O_2 contents. Increased starch hydrolysis by β-amylase increased the seed germination rate (Zhang et al. 2008, 2010). Exogenous H_2S provoke some signaling molecules which increased cell division rate in roots and increased adventitious root growth.

Exogenous H_2S application alleviates biotic and abiotic stress in plants. Earlier research only associated it with defense system in plants during pathogenic attacks (Bloem et al. 2004). Later in 2008, study revealed its protective effect against copper (Cu) toxicity (Zhang et al. 2008). After that, studies showed positive response of H_2S application in alleviating the metal stress (e.g., aluminum, chromium, zinc, boron, and cadmium), drought, temperature, and nutrient stress in various plants as described in Table 2. H_2S regulates homeostasis process in cells. During drought stress, it accumulates osmolytes proline and trehalose, which protect plants from drought effects. It is also involved in the stomata closing process, reducing the amount of water transpired by the plant under both normal and stressed conditions, thus increasing overall photosynthesis efficiency (Iqbal 2018). H_2S also mediates stomatal opening by downregulating the ethylene-induced NO accumulation in stomatal cells (Liu et al. 2011; Iqbal 2018).

Several studies pointed to an inter-relationship between H_2S and other plant hormones such as gibberellic acid, abscisic acid, and ethylene and modulate their signaling process (Hasanuzzaman et al. 2018). H_2S controls the induction of abscisic acid (ABA) in plants. Studies highlighted the effect of increased ABA synthesis at high H_2S concentration (Jin et al. 2011). High atmospheric or intracellular H_2S concentration in plants influences ABA

Table 2 Various studies indicating the signaling role of H_2S in plant growth improvement under abiotic and biotic stress conditions

Plant species	H_2S donor	Plant response	References
Strawberry	NaHS	Increase shelf life of harvested fruit and reduce rottening	Hu et al. (2012)
Maize	NaHS	Increase seed germination under heat stress	Li et al. (2013)
Bean, corn and wheat	Dissolved H_2S	Germination rate, increase seedling size and improve growth	Dooley et al. (2013)
Cotton	NaHS	Mitigate lead induced changes in plant and improve plant growth, chlorophyll contents and photosynthesis rate	Bharwana et al. (2014a,2014b)
Rice	NaHS	Improve photosynthesis rate and stomatal density	Duan et al. (2015)
Maize	NaHS	Increase plant tolerance against chromium toxicity and increase antioxidant enzyme activities	Kharbech et al. (2017)
Tomato	NaHS	Antagonize ethylene effect and delayed ripening of postharvest tomato	Yao et al. (2018)
Strawberry	NaHS	Alleviate iron deficiency effects	Kaya and Ashraf (2019)
Barley	NaHS	Reduced Cd toxicity and malondialdehyde and increase superoxide dismutase activity and chlorophyll contents	Fu et al. (2019)
Alfalfa	NOSH	Increased drought tolerance and reduce malondialdehyde production and increase superoxide dismutase activity	Antoniou et al. (2020)
Blueberry	NaSH	Improve tolerance of temperature stress and increase photosynthesis rate	Tang et al. (2020)
Arabidopsis haliana	Endogenous H_2S	Reduce cadmium and reactive oxygen species contents	Zhang et al. (2020)
Avocado	NaSH	Protect plant from frost and high light intensity	Joshi et al. (2020)

receptor expression and upstreams the ABA accumulation. This initiates signals for stomata closure, reduced water loss, and protection of plants from drought (Jin et al. 2013; Antoniou et al. 2020). Exposure of plant to ethylene initiates H_2S synthesis in plants (Liu et al. 2011). Exposure of some plants with H_2S increases indole acetic acid production (Zhang et al. 2009a, b). However, H_2S alleviates the negative effect of jasmonic acid and gibberellic acid through signal transduction process (Xie et al. 2014; Hou et al. 2011). Jasmonic acid increases H_2O_2 contents in plants causing closure of stomata. H_2O_2 is another signaling molecule inter-related with H_2S. There are plenty of evidences that proved these both signaling molecules have antagonistic effects (Hou et al. 2011), but few studies showed that seed priming with H_2O_2 improves H_2S contents in endosperm and increases germination rate of *Jatropha curcas* (Li et al. 2012a, b). However, under plant stress conditions, H_2S improves antioxidant system (Tang et al. 2020; Zhang et al. 2020).

Contrary effect of H_2S is also reported with NO (signaling molecule). In *Arabidopsis thaliana*, application of NaSH reduced NO accumulation in epidermal cells due to increased H_2S activity. Molecular analysis denoted that both NaSH and GYY4137 reduced the NO activity up to a large extent (Lisjak et al. 2010). H_2S also inter-relates with Ca-signaling pathways. Calcium maintains the permeability and rigidity of cell wall. Pre-treatment of tobacco with NaSH improves Ca^{2+} uptake in plants through upstreaming of calmodulin (Li et al. 2013). Under metal toxicity, H_2S ameliorates the plant tolerance by increasing proline contents. In short, H_2S protects plant against biotic and abiotic stress and improves the growth of plants (Fu et al. 2019).

Hydrogen Sulfide and Abiotic Stress

Climate change is one of the significant factors that affect plant health and results in a decrease in production. Climate change imposes different environmental stresses on plants, i.e., salt stress, water deficit, extreme temperatures, and nutritional imbalance (Khalid et al. 2019). When the plants are exposed to these kinds of stresses, they generally increase the production and accumulation of reactive oxygen species (ROS), i.e., hydroxyl radicals, hydrogen peroxide, and superoxide ions in cells. To make the equilibrium in the cells, plant increases the activity of specific antioxidant enzymes, osmolytes, which decrease the accumulation of ROS (Suzuki et al. 2012).

In previous years, several reports have emphasized the impact of exogenous application of hydrogen sulfide on plants and their response to different environmental stresses, mainly its contribution in the regulation of cell signaling metabolism, upregulation, downregulation of gene expressions, and the activation of different antioxidant enzymes and osmolytes (Singh et al. 2019). Previous scientists also described a swift accumulation of endogenous hydrogen sulfide under different abiotic stress conditions to levels that trigger physiological responses (Fang et al. 2014; Lai et al. 2014). However, the molecular responses and signal transduction metabolism of hydrogen peroxide in plants are still elusive. The information on these metabolisms and the alterations that are carried out in different environmental conditions is essential to recognize how plants adequately respond to their environment.

Low temperature or cold stress significantly affects the plant's growth and development directly by constraining enzyme activities and metabolic reactions and, indirectly, through cold-induced osmotic stress (inhibition of water uptake and cellular dehydration) and oxidative stress (Chinnusamy et al. 2007). Hydrogen sulfide was stated to alleviate osmotic and oxidative stresses induced under cold or low-temperature stress by modifying the antioxidant enzymes activities, accelerates the accumulation of osmoprotectants (proline, total soluble sugars), and decreases cell membrane permeability (Shi et al. 2013). The mitogen-activated protein kinase (MAPK) pathway was also observed to be involved in the hydrogen sulfide-mediated response of Arabidopsis seedlings to low-temperature stress, with a specific effect on stomatal opening.

High temperature, water deficiency, and salt stress have reached an alarming concern in the context of environmental change (Hussain et al. 2018; Khalid et al. 2020). High temperature strictly affects plant growth and development, resulting in a substantial decline in yield (Akter and Islam 2017). The tolerance of plants against high temperatures is also improved by hydrogen sulfide. Numerous studies have delivered confirmation that the addition of sodium hydrogen sulfide, a hydrogen sulfide donor, improves plant germination and tissue viability (Li et al. 2013) and decreases the adverse phenotypic effects of high temperature such as wilting and curling of leaves (Christou et al. 2014). Different mechanisms of different plants against heat stress were reported: in corn, the hydrogen sulfide-induced tolerance, which was arbitrated by an increase in salicylic acid (SA) and proline (Li et al. 2015); in tobacco, it was suggested that hydrogen sulfide adjusts the entry of extracellular calcium ions across the plasma membrane by a direct effect on calmodulin (ubiquitous calcium-binding protein) (Li et al. 2012a, b). In strawberry, hydrogen sulfide alleviated oxidative stress. It helped to preserve root tissues against heat-induced damage by inducing gene expression of several antioxidants and heat shock proteins, including catalase, superoxide dismutase, HSP70, HSP80, and HSP90 (Christou et al. 2014).

The involvement of hydrogen sulfide in plant responses to water deficit has also been widely evaluated. It mainly depends on how much time and what concentration of heat was applied, hydrogen peroxide may encourage the closure or aperture of stomata. Both effects are mediated by a signaling molecule and involves the activity of calcium ion, cADP ribose, and slows anion channel 1 (Honda et al. 2015).

By knocking down the L-cysteine desulfhydrase in Arabidopsis plants, Jin et al. (2013) studied the function of hydrogen sulfide in stomatal movement and the relationship between hydrogen sulfide and abscisic acid metabolism in signaling transduction. They concluded that hydrogen sulfide is involved in the expression regulation of abscisic acid receptor candidates and potassium ions and calcium ion channels in guard cells. In addition to stomatal movement, numerous works have reported that hydrogen sulfide helps to provide tolerance to drought through the accumulation of osmolytes like proline and the association of calcium messenger system (Li et al. 2014).

Heavy metals such as cadmium, chromium, copper, and zinc are highly toxic for plants. Their accumulation in the intracellular compartments can cause DNA damage, enzyme

Table 3 Endogenous H_2S production in plants triggered under various abiotic stresses

Species	Stress	H_2S contents		References
		Without stress	With stress	
Rice (*Oryza sativa*)	Cd	5 μmol g^{-1} (FW)	6 μmol g^{-1} (FW)	Mostofa et al. (2015)
Chinese cabbage (*Brassica rapa*)	Cd	0.38 nmol mg^{-1} (Pr min^{-1})	0.58 nmol mg^{-1} (Pr min^{-1})	Zhang et al. (2015)
Foxtail millet (*Setaria italica*)	Cr6+	0.6 nmol mg^{-1} (Pr min^{-1})	1.6 nmol mg^{-1} (Pr min^{-1})	Fang et al. (2014)
Alfalfa (*Medicago sativa*)	NaCl	30 nmol g^{-1} (FW)	70 nmol g^{-1} (FW)	Lai et al. (2014)
Strawberry (*Fragaria × ananassa*)	PEG-6000, NaCl	25 nmol g^{-1} (FW)	35 nmol g^{-1} (FW)	Christou et al. (2013)
Arabidopsis (*Arabidopsis thaliana*)	Drought	6 nmol mg^{-1} (Pr min^{-1})	14 nmol mg^{-1} Pr min^{-1})	Jin et al. (2011)
Arabidopsis (*Arabidopsis thaliana*)	Cold	3 nmol g^{-1} (FW)	5 nmol g^{-1} (FW)	Shi et al. (2015)
Grape (*Vitis vinifera*)	Cold	7 μmol g^{-1} (FW)	15 μmol g^{-1} (FW)	Fu et al. (2013)
Bermudagrass (*Cynodon dactylon*)	Cold	5 nmol g^{-1} (FW)	14 nmol g^{-1} (FW)	Shi et al. (2013)
Lamiophlomis rotata	Cold	12 nmol g^{-1} (FW)	24 nmol g^{-1} (FW)	Ma et al. (2015)
Tobacco (*Nicotiana tabacum*)	Heat	2 nmol g^{-1} (FW)	8 nmol g^{-1} (FW)	Chen et al. (2016)
Barley (*Hordeum vulgare*)	UV-B	125 nmol g^{-1} (FW)	230 nmol g^{-1} (FW)	Li et al. (2016a)
Pea (*Pisum sativum*)	Hypoxia	0.8 μmol g^{-1} (FW)	1.5 μmol g^{-1} (FW)	Cheng et al. (2013)

FW fresh weight, *Pr* protein

inactivation, protein oxidation, and lipid peroxidation. The role of hydrogen sulfide in plant response to heavy metal stress has been recently reviewed by Hancock and Whiteman (2015) and Li et al. (2016b) (Table 3). In cucumber seedlings, pre-treatment with sodium hydrogen sulfide altered the expression of cell wall-associated proteins such as PME (CsPME) and expansin (CsExp), leading to the alleviation of boron-induced toxicity. Similarly, sodium hydrogen sulfide alleviated the inhibitory effects of copper and reduced the visible symptoms in germinated seeds and radical tips.

The roots are important plant organs for anchoring and nutrient and water uptake. Therefore, fast growth and development of root is essential for crop survival in stressful conditions. The knowledge about impact of H_2S on roots formation and growth pattern is very important for stress tolerance. Several researchers reported positive impacts of application of this molecule on root of raddish (Carter et al. 2018), sweet potato, willow and soybean (Zhang et al. 2009a, b), and Chinese crab apple (Wei et al. 2017) and these are mainly as a result of H_2S interaction with Indole Acetic Acid (IAA), Nitric Oxide (NO), Hydrogen per Oxide (H_2O_2), and Malondialdehyde (MDA) (Zhang et al. 2009a, b, Mei et al. 2017, Ma et al. 2016a, b). The pretreated seedlings with NaHS upregulated abscisic acid (ABA) biosynthesis in roots during drought. Moreover, the exogenous application of ABA increased the H_2S contents in the roots in drought, and it showed cross talks between these two molecules (Ma et al. 2016a, b). The presence of excessive salt in soil resulted in salinity stress which disupts nutrients and water uptake along with oxidative damages and produces poor yield. The H_2S mediates the NO production which is further utilized for maintaining ion (K^+/Na^+) homeostatis to improve salt tolerance (Chen et al. 2015).

Molecular Mechanism and Biosynthesis of H_2S in Plants

Hydrogen sulfide gaseous signaling molecule is involved in the growth and development of plants. It regulates different physiological processes in plants, including germination, lateral and adventitious root formation, stomatal conductance and photosynthesis (Duan et al. 2015; Jia et al. 2015; Liu and Lal 2015; Jin and Pei 2016; Li et al. 2016a, b). Plant response to abiotic stress is also regulated by H_2S and thus considered as versatile regulator (Guo et al. 2015). The emission of H_2S in plant was first observed by DeCormis in 1968 (Rennenberg, 1989). Exposure of some plants e.g., pumpkin, cantaloupe, corn, cucumber, and soybean to light results in the synthesis of H_2S as reported by Wilson et al. (1978). Similarly, emission of H_2S in cucumber leaf tissue was reported earlier (Sekiya et al. 1982).

H_2S is recognized as an important secondary messenger in various plant developmental processes, stress responses, and due to its small size it can easily navigate between cells. Thus, it behaves as a gasotransmitter at lower cellular concentrations. It does not require any transporter assistance; therefore, it can move through hydrophobic plasma and organelle membranes (Mathai et al. 2009; Shivaraj et al. 2020). Hydrogen sulfide accumulation occurs in chloroplasts via a photosynthetic sulfate assimilation pathway, and the reaction is triggered by sulfide reductase (SiR) (Garcia et al. 2015). The cytosolic hydrogen sulfide is accumulated mainly with the action of the enzyme L-cysteine desulhydrase 1 (DES1), and it is of interest that the sulfide concentration in chloroplasts is always higher than in cytosol (Kabil and Banerjee 2010).

Multiple enzymatic systems are involved in the biosynthesis of H_2S in plants. According to Aroca et al. (2015), H_2S production mainly occurs in the chloroplast and partly in the mitochondria and cytosol. It includes sulfite reductase (SiR), L-Cysteine desulfhydrase (LCD), D-Cysteine desulfhydrase (DCD), cysteine synthase (CS), beta-cyanoalanine synthase (CAS), carbonic anhydrase, Nitrogenase Fe-S cluster (NFS 1& 2), O-acetyl-L-serine (thiol) lyase (OASTL), and Desulfhydrase (DES1). The enzymatic role in various steps of synthesis of H_2S is shown in Fig. 4. L-Cysteine desulfhydrase is the major player involved in the production of H_2S as it catalyzes the conversion of L-Cys to pyruvate, NH^{4+} , and H_2S as shown in Fig. 4. The cofactor in this reaction is pyridoxal phosphate (Gotor et al. 2015). Similarly, D-Cys is converted to pyruvate, ammonia, and H_2S in the cytoplasm through DCD (Riemenschneider et al. 2005).

Until today, there are six different pathways reported in the plants through which H_2S has been generated. Firstly, SO_4^{2-} is reduced to S^{2-} and then it became a part of organic metabolites. Before this reduction reaction, SO_4^{2-} is activated by adenylation to form adenosine 5′ phosphosulfate (APS), which is catalyzed by ATP sulfurylase (ATPS). APS reductase (APR) enzyme in plastid converts APS to sulfite that is further reduced to sulfide and H_2S through ferredoxin-dependent sulfite reductase (SiR) enzyme (Fig. 4). At the end, sulfide is incorporated into amino acids skeleton of OAS (O-acetylserine) by OAS-TL (O-acetylserine thiol lyase) to form cysteine. The revers of this reaction generates H_2S (Li 2015). In these all reactions, OAS is product of serine and catalyzed by SAT (serine acetyltransferase). H_2S, pyruvate, and NH_4^{+1} synthesis due to the degradation of L-Cysteine were first reported by Harrington and Smith (1980). Xie et al. (2013) found that H_2S in higher plants was produced by enzymatic reaction of LCD on substrate L-cysteine. Furthermore, L-cysteine was converted to L-alanine and elemental S through the action of enzyme LCD. The elemental S could be further reduced to H_2S if reductant is present (Papenbrock et al. 2007a, b).

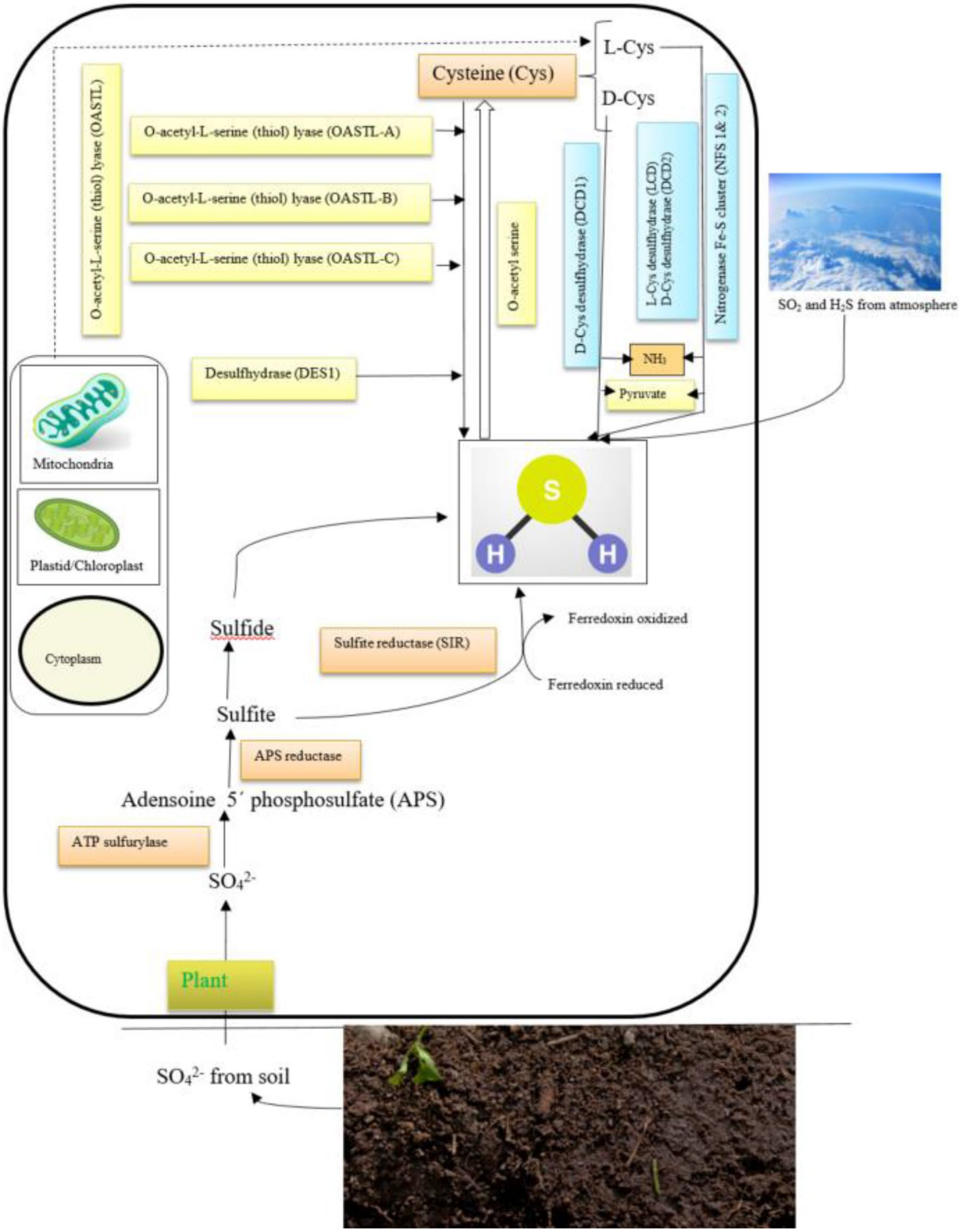


Fig. 4 Hydrogen sulfide (H_2S) generation mechanism in plants (Adapted from Papenbrock et al. 2007a, b)

Léon et al. (2002) reported two genes (AtNFS1 and AtNFS2) that encoded NifS-like cysteine desulfurase catalyzing cysteine to form H_2S. D-cysteine could also be catalyzed by DCD to generate H_2S as reported by Riemenschneider et al. (2005) in their study on Arabidopsis thaliana. The subcellular localization, enzymatic inhibitors, and substrates for both LCD and DCD seem different. Another enzyme, i.e., b-cyanoalanine synthase (CAS) can also act on L-Cysteine and cyanide to form H2S and b-cyanoalanine as reported by Hatzfeld et al. (2000). Similarly, it has been found that three genes, i.e., CYSC1,CYS-D1, and CYS-D2 encode enzyme CAS that confirm that L-Cysteine is involved in the synthesis of H_2S (Jost et al. 2000). The enzyme cyanoalanine synthase cI (CAS-CI) also produces hydrogen sulfide in the mitochondria during the synthesis of β-cyanoalanine (Yamaguchi et al. 2000).

Hydrogen Sulfide and its Interaction with Other Signaling Molecules During Plant Abiotic Stress

Hydrogen sulfide has been considered as a toxic gas for living organisms; however, it has emerged as a new molecule in living cells for signaling, considering equally crucial as hydrogen peroxide (H_2O_2), carbon monoxide (CO), and nitric oxide (NO) (Kimura 2014). Hydrogen sulfide is a major component in plant responses against stress. Many stresses may result in an increase in hydrogen sulfide in plants, and this may result in the mediation of cell stress by different cellular metabolisms (Fig. 5).

Numerous reports have been available on this gasotransmitter related to the growth of vegetative plants and affecting the disease resistance, protective roles against stresses such as oxidative stresses (Fang et al. 2016), drought and heat tolerance (Li et al. 2012a, b; Shen et al. 2013), osmotic and saline stresses, stomatal closure/aperture (Papanatsiou et al. 2015), modulating in photosynthetic machinery (Chen et al. 2011), and autophagy regulation (Laureano-Marin et al. 2016).

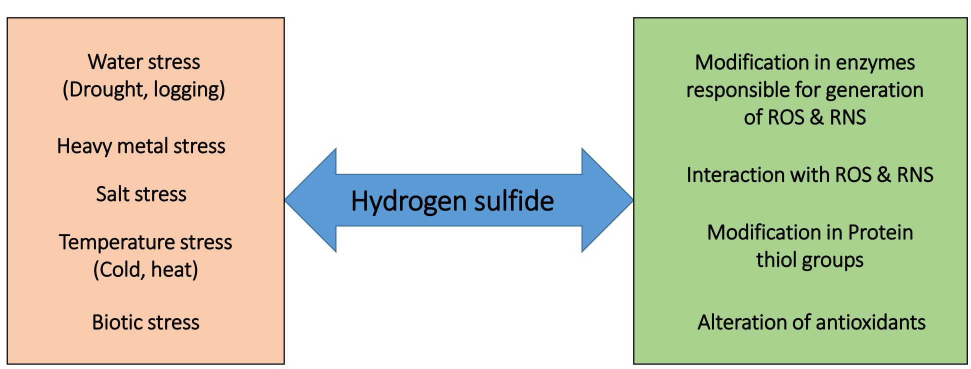
Moreover, hydrogen sulfide is a reactive molecule to alter the signals concerning the plant hormones (Liu et al. 2011; Lisjak et al. 2010a; Zhang et al. 2010). Concerning the primary mechanism of action, a post-translational modification (PTM) of proteins (persulfidation) is formed when the conversion of the thiol group ($^{-}$SH) into the persulfide group ($^{-}$SSH) occurred at the reactive cysteine residues on the target proteins. Persulfidation showed an increased nucleophilicity than the thiol group; thus, modified cysteines demonstrated a more significant challenge activity leading to a higher percentage of proteins compared to the reactive nitrogen and oxygen species. The modified targets of hydrogen sulfide is unclear; however, the sulfane-sulfur atom has a unique ability to bind reversibly to other sulfur atoms to generate hydrosulfides and polysulfides. Polysulfides seemed to be effective in the persulfidation since these are more nucleophilic than hydrogen sulfide (Toohey 1989). These newly emerged low molecular weight compound persulfides are the potential mediators in sulfide signaling. In conclusion, the extent of the interaction between signaling molecules needs more study on the biochemical cascade triggered in the plant cells toward different stress conditions. Hydrogen peroxide molecules are small in size and have ability to cross by cellular membranes and its movement also occurs through aquaporin channels in different compartments of cells. Hydrogen sulfide is also involved in feeding of electrons in complex II of mitochondria by enzyme quinone oxidoreductase. Hydrogen sulfide also involved in regulation of phosphorylation of the plasma membrane to maintain homeostasis of ions (Li et al. 2013).

The optimum concentration of hydrogen sulfide will increase growth and activate different metabolisms. However, variation in the concentration of hydrogen sulfide will ultimately restrict the development of primary roots (Zhang et al. 2017). Hydrogen sulfide toxicity repressed primary root growth by triggering a signal transduction pathway involving reactive oxygen species (ROS) accumulation, MITOGEN-ACTIVATED PROTEIN KINASE 6 (MPK6) activation,, and nitric oxide (NO) production.

Conclusion and Future Perspectives

The role of H_2S is alleviating various stresses through endogenous production and exogenous application is quite clear. The literature highlighted that advent of biotic and abiotic stress stimulates the generation of H_2S to provide protection against damages imposed by stress and is even helpful for protection against diseases. There is detailed description of alleviating the role of H_2S against heavy

Fig. 5 Modifications in cellular reactions by hydrogen sulfide under stress



metals, salinity, drought, and water logging and others. It is a potential tool for preservation of post-harvest fruit quality.

The phytotoxic and beneficial impacts of H_2S largely depend upon the dose, the detailed research on dose standardization for various crops should be focused for its practical application in agriculture. It is still unknow that the actual site of H_2S production in plants and its interaction with other molecules in plant metabolism (Corpas and Palma 2020). The H_2S and NO displayed interplay with each other and biochemical basis of interplay still need to be worked out for deep understanding of the phenomenon. Suppose H_2S is endogenously produced as signaling molecules, then it should be measured. Furthermore, considering H_2S signaling molecules, its production should be stopped when not needed. Because plants remove H_2S when it is just a pollutant, the process of removal of H_2S still needs to be studied (Lisjak et al. 2013).

Although H_2S is widely being used for improving post-harvest quality of climacteric and non-climacteric fruits, understanding the mechanism of signaling H_2S with fruit ripening is required for future investigation (Ziogas et al. 2018). Although detail studies on role of H_2S in fruits have been carried out and its practical application has been suggested regarding preservation of post-harvest fruit quality, the exact biochemical basis of interaction of H_2S with NO should be exploited (Ziogas et al. 2018). The levels of biological sulfide measuring techniques differ greatly according to testing procedure. The future investigation is required for uniform readings. Keeping in view the phytotoxicity, the crops like brassica species may be grown in areas where H_2S concentration is high in atmosphere (Ausma and Kok 2019).

Author Contributions For research articles with several authors, a short paragraph specifying their individual contributions must be provided. The following statements should be used: Conceptualization MA, SF, and SA; methodology MA, SH, MT, FI, and SU; software SA; validation HMH and WN; formal analysis CW; resources HL; writing—original draft preparation MA, SF, and SA; writing—review and editing, SF and MA; visualization SF, and supervision SF.

Compliance with Ethical Standards

Conflict of interest Authors declare that they have no conflict of interest.

Ethical Approval This article does not contain any studies with human participants or animals performed by any of the authors.

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Affiliations

Mukhtar Ahmed[1,2] · Shah Fahad[3,4] · Muhammad Arif Ali[5] · Sajjad Hussain[6] · Muhammad Tariq[7,8] · Fariha Ilyas[5] · Shakeel Ahmad[7] · Shah Saud[9] · Hafiz Mohkum Hammad[10] · Wajid Nasim[11] · Chao Wu[12] · Hongyan Liu[3]

Shakeel Ahmad
shakeelahmad@bzu.edu.pk

1 Department of Agronomy, Pir Mehr Ali Shah, Arid Agriculture University, Rawalpindi, Pakistan

2 Department of Agricultural Research for Northern Sweden, Swedish University of Agricultural Sciences, Uppsala, Sweden

3 Hainan Key Laboratory for Sustainable Utilization of Tropical Bioresource, College of Tropical Crops, Hainan University, Haikou 570228, Hainan, China

4 Department of Agronomy, The University of Haripur, Haripur, Khyber Pakhtunkhwa 22620, Pakistan

5 Department of Soil Science, Bahauddin Zakariya University, Multan, Pakistan

6 Department of Horticulture, Bahauddin Zakariya University, Multan, Pakistan

7 Department of Agronomy, Bahauddin Zakariya University, Multan, Pakistan

8 Agronomy Section, Central Cotton Research Institute, Old Shuja Abad Road, Multan, Pakistan

9 Department of Horticultural, Northeast Agricultural University, Harbin 150030, China

10 Department of Environmental Sciences, Comsats University Islamabad, Islamabad, Pakistan

11 Department of Agronomy, University College of Agriculture and Environmental Sciences, The Islamia University of Bahawalpur (IUB), Bahawalpur, Pakistan

12 Guangxi Institute of Botany, Chinese Academy of Sciences, Guilin, China