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The Role of Hydrogen Sulfide in Plants Exposed to Heavy Metal Stress

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Abstract

Hydrogen sulfide (H_2S) with its characteristic odour has been known for centuries as a toxic gas for animals and human, especially at higher concentration. It has been also demonstrated that it can be phytototoxic resulting in disorders of the development but lower amounts of this gas may have beneficial effects on plants exposed to several abiotic stress factors such as salinity, drought, heat or heavy metal stress [1]. It seems that the activation of the antioxidant system triggerred by H_2S is responsible of the tolerance in H_2S-treated plants [2]. In this mini-review, we try to give an overview of the potentially positive and protective roles of H_2S in plants under metallic stress.

Keywords: Hydrogen sulfide; Gasotransmitter; Heavy metal stress; Nitro-oxidative stress; Tolerance

Abbreviations

AOA: Aminooxyacetic Acid; APX: Ascorbate Peroxidase; AsA: Ascorbic Acid; CAS: Cyanoalanine Synthase; CAT: Catalase; Chl: Chlorophyll; CO: Carbon Monoxide; CS: Cysteine Synthase; Cys: Cysteine; D-DES: D-Cysteine Desulfhydrase; DHAR: Dehydroascorbate Reductase; GPX: Glutathione Peroxidase; H_2O_2: Hydrogen Peroxide; L-DES: L-Cysteine Desulfhydrase; DES: Cysteine Desulfhydrase; GR: Glutathione Reductase; GSH: Glutathione (reduced); GST: Glutathione-S-Transferase; GYY4137: Morpholin-4-ium 4-methoxyphenyl (morpholino) Phosphinodithioate; H_2S: Hydrogen Sulfide; HT: Hypotaurine; MDA: Malondialdehyde; MDHAR: Monodehydroascorbate Reductase; MT: Metallothionein; NaHS: Sodium hydrosulfide; NO: Nitric Oxide; PAG: Propargylglicine; PCs: Phytochelatins; POD: Peroxidase; Pro: Proline; ROS: Reactive Oxygen Species; RNS: Reactive Nitrogen Species; RSS: Reactive Sulphur Species; SOD: Superoxide dismutase; SNP: Sodium nitroprusside.

Introduction

Hydrogen sulfide (H_2S), a colourless gas with a small molecular size and a typical odour reminding to rotten egg, has been known to be toxic for animal and human at higher levels. At the same time, it was discovered that the presence of this gas has effects on plants' physiological processes, such as photosynthetic activity, development or stress tolerance [3,4]. Lower concentrations of exogenous H_2S, mainly derived from sodium hydrosulfide (NaHS) as donor, might have beneficial influences on plant growth and development [1], while excess H_2S can be deleterious, as it was demonstrated in *Arabidopsis* treated with 200-800 µM NaHS [5].

It is well-known that certain thermal fountains and the typically sulphur emitting vulcanic vents (solfataras) are natural sources of hydrogen sulfide but it can be produced swamps or sewers due to sulfate- or sulfur-reducing microorganisms [6]. Besides, several industrial technologies e.g. in oil refineries produce this gas as a by-product causing serious toxicity problems [7].

H_2S is the third gasotransmitter which was discovered in the 2000s and similar to Nitric Oxide (NO) and Carbon Monoxide (CO) it was firstly detected in animal and human [8]. Several studies confirmed that H_2S arises endogenously mainly in cerebral tissues and has numerous functions e.g. in neuromodulation, cardiovascular or neurodegenarative diseases [3,4]. Up to now many researchers exhibited that this gaseous molecule also has a remarkable cue in plant physiological processes such as seed germination, morphogenesis of root, photosynthesis, senescence or stomatal closure [9,10]. Moreover, it might have a key role in plant tolerance against nitro-oxidative stress trigerred by biotic e.g. pathogens, [11] or abiotic factors like drought, excess salinity or Heavy Metals (HMs) [12,13]. Since the emission and circulation of HMs in food chain are still great challenges globally, it is useful to overview the results about the changes of H_2S level in plants exposed to HM stress and the potentially beneficial exogenous application of H_2S, as well.

The Role of H_2S in Plants at Physiological Conditions

In plants, cysteine Desulfhydrases (DES) are considered to be the key enzymes of H_2S synthesis catalyzing the production of H_2S from L- or D- Cysteine (L-Cys and D- Cys) [1]. L-Cys Desulfhydrases (L-DES, EC 4.4.1.28.) use L-Cys as substrate creating H_2S, pyruvate and ammonia and are mainly located in the cytosol, nucleus and mitochondria, whilst D-Cys Desulfhydrases (D-DES, EC 4.4.1.15.) degrade D-Cys and can be found in mitochondria [2,4]. On the contrary, earlier summary by Guo et al. [3] reported that the main location of D-DES enzymes is the cytoplasm and L-DESs are localized in the chloroplasts and mitochondria. The activity of L-DES enzymes have been already characterized in tobacco, pumpkin, cucumber, *Arabidopsis* and *Brassica napus* [14,3]. Cytosolic D-DES activity was exhibited in pumpkin, cucumber, spinach, tobacco and *Arabidopsis* [3,4]. Another difference between L- and D-DES enzymes is that the activity of L-DESs can be inhibited using Aminooxyacetic Acid (AOA) while it has no influence on D-DESs [3]. Not only DES enzymes ara capable of producing H_2S in plant cells, but chloroplastic

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Table 1: The effects of H_2S supplementation under HM stress in plants.

Name of HM	Plant name	Concentration or degree of the HM stress	Time of HM exposure	Chemical form, concentration and duration of H_2S application	Plant organ investigated	Effects of exogenous H_2S treatment*	Reference
Essential HMs							
Cu	*Triticum aestivum* L. Luomai 9133	100 mM (hydroponic)	24 h	0.4-1.6 mM NaHS, 12 h (pre-treatment)	leaves	Activity of antioxidant enzymes (GR, APX, DHAR, MDHAR) ↑; GSH and AsA content ↑	[47]
	Triticum aestivum L. cv. Luomai 9133	20 mM (hydroponic)	24 and 48 h	0.4, 0.8 and 1.2 mM NaHS, 12 h (pre-treatment)	leaves	Activity of antioxidant enzymes (GPX, SOD, APX, GR) ↑; LP ↓; H_2O_2 content ↓ at 0.4 and 0.8 mM NaHS	[48]
Zn	*Capsicum annuum* L. cv. Semerkand	0.05 and 0.5 mM (hydroponic)	10 weeks	0.2 mM NaHS, 10 weeks (co-treatment)	leaves	Chl content ↑; POD activity ↑; SOD activity ↑; CAT activity ↑; LP ↓; H_2O_2 content ↓; Pro ↓	[49]
	Solanum nigrum L.	400 mM (hydroponic)	5 days	50-400 mM NaHS, 12 h (pre-treatment) or 5 days (co-treatment)	root	Zn uptake ↓; L-DES activity ↑ after NaHS pretreatment; L-DES activity ↑ns after 100-200 mM NaHS co-treatment; no change in biomass	[40]
					leaves	Zn accumulation ↓; L-DES activity ↑ after NaHS pretreatment; L-DES activity ↑ns after 100-200 mM NaHS co-treatment; no change in biomass	
Non-essential HMs							
Cr	*Arabidopsis thaliana* ecotype Col-0	100-500 mM (*in vitro*, MS medium)	5 days	50 mM NaHS (pre-treatment), 3 days	seedlings	Root elongation ↑; LP ↓; GSH content ↑; synthesis of MT and PCs ↑	[43]
	Brassica oleracea var. botrytis	10-200 mM (pot experiment, soil)	4 weeks	200 mM NaHS as foliar spray (twice)	leaves	Activity of antioxidant enzymes (CAT, SOD, POD, APX) ↑; LP ↓; H_2O_2 content ↓; Cr uptake ↓ns at 10-100 mM Cr	[50]
					roots	Activity of antioxidant enzymes (CAT, SOD, POD, APX) ↑; LP ↓; H_2O_2 content ↓; Cr uptake ↓ ns only at 100 mM Cr	
	Hordeum vulgare L. genotype Hua 30	100 mM (hydroponic)	40 and 60 days	100 and 200 mM NaHS (co-treatment)	leaves	Photosynthetic activity ↑; Cr uptake ↓; plant height ↑	[42]
					roots	Cr uptake ↓	
	Setaria italica L. ecotype Jingu-21	5 mM (*in vitro*)	12 and 24 h	50 mM NaHS, 12 h (pre-treatment)	leaves	H_2O_2 content ↓; Cr-tolerance ↑; LP ↓; activity of SOD and POD ↓; GSH and AsA content ↑	[51]
	Triticum aestivum L. cv. Yangmai 158	0.5-6 mM (*in vitro*)	48 h	0.4-2 mM NaHS, 12 h (pre-treatment)	seedlings	Activity of antioxidant enzymes (CAT, SOD, POD, APX) ↑; LP ↓; H_2O_2 content ↓	[52]
Cd	*Brassica napus* L. cv. ZS 758	100 and 500 mM (hydroponic)	15 days	100 and 200 mM NaHS (co-treatment)	leaves	Photosynthetic activity ↑; Cd content ↓; plant height ↑; ROS production ↓; LP ↓; activity of antioxidant enzymes (APX, CAT, SOD, POD, GR) ↑	[34]
					roots	Cd uptake ↓; root length ↑; ROS production ↓; LP ↓; activity of antioxidant enzymes (APX, CAT, SOD, POD, GR) ↑	
	Brassica napus L. "Xikou huazi"	20 mM (hydroponic)	7 days	50 mM NaHS, 6 h (pre-treatment)	leaves	Chl content ↑; Cd content ↓;	[28]
					roots	Root biomass ↑; L-DES activity ↑; CAS activity ↑ns; Cd uptake ↑; Cd binding capacity of root cell walls ↑	
	Brassica rapa L. ssp. pekinensis (Jinyu75)	5, 10 and 20 mM (soil)	48 h	5 mM NaHS, 24 h (pre-treatment)	roots	Root length ↑; ROS production ↓; LP ↓; activity of SOD and CAT ↑, while that of POD ↓ns, no change in APX activity	[53]
	Cucumis sativus L. var. Wisconsin	10, 50, 100 and 150 μM (hydroponic)	2 or 24 h	100 mM NaHS (co-treatment)	leaves	Photosynthetic activity ↑	[54]
					roots	H_2O_2 content ↓ns	
	Medicago sativa L. Victoria	200 μM (hydroponic)	12 h	100 mM NaHS, 6 h (pre-treatment)	roots	Root elongation ↑; LP ↓; GSH ↑ns; ROS production ↓	[55]
	Salix matsudana L.	5, 10 and 30 μM (hydroponic)	60 days	0.3 mM NaHS, spraying 1x	leaves	Leaves biomass ↑; Cd content ↓ns; Cd binding capacity of the cell walls ↑; GSH content ↑; LP ↓; H_2O_2 content ↓	[56]

					roots	Root biomass ↑; Cd uptake ↓ns; Cd binding capacity of root cell walls ↑; GSH content ↑; LP ↓; H_2O_2 content ↓; activity of antioxidant enzymes (CAT, SOD, POD) ↑	
Pb	*Brassica napus* L. cv. ZS 758	100 and 400 mM (hydroponic)	15 days	100 and 200 mM NaHS (co-treatment)	leaves	plant biomass ↑; Chl and carotenoid content ↑; macro- and micronutrient content ↑; ROS level ↓, LP ↓; activity of antioxidant enzymes (CAT, SOD, POX, APX) ↑	[35]
					roots	macro- and micronutrient content ↑; ROS level ↓, LP ↓; activity of antioxidant enzymes (CAT, SOD, POX, APX) ↑	
	Brassica napus L. cv. ZS 758	100 and 400 mM (hydroponic)	15 days	100 and 200 mM NaHS (co-treatment)	shoot	Pb accumulation ↓; plant height ↑; net photosynthetic rate ↑	[41]
					roots	Pb uptake ↓; root length ↑	
	Gossypium hirsutum L. genotype MNH 886	50 and 100 mM (hydroponic)	45 days	200 mM NaHS (co-treatment)	leaves	Pb accumulation ↓; plant height ↑; Chl and carotenoid content ↑; activity of antioxidant enzymes (CAT, SOD, POD, APX) ↑; LP ↓	[57]
					roots	Pb uptake ↓; root length ↑; activity of antioxidant enzymes (CAT, SOD, POD, APX) ↑; LP ↓	
Al	*Brassica napus* L. cv. ZS 758	0.1 and 0.3 mM (hydroponic)	15 days	0.3 mM NaHS (co-treatment)	leaves	Al accumulation ↓; plant height ↑; net photosynthetic rate ↑; Chl and carotenoid content ↑; macro- and micronutrient content ↑; ROS level ↓, LP ↓; activity of antioxidant enzymes (CAT, SOD, POD, APX, GR) ↑	[46]
					roots	Al uptake ↓; root length ↑; macro- and micronutrient content ↑; ROS level ↓, LP ↓; activity of antioxidant enzymes (CAT, SOD, POD, APX, GR) ↑	
	Hordeum vulgare L. var. ZAU 3	100 mM (hydroponic)	24 h	200 mM NaHS, 24 h (pre-treatment)	roots	Al uptake ↓; root length ↑; LP ↓	[45]
			25 days	100, 200 and 400 mM NaHS (co-treatment)	leaves	Net photosynthetic rate ↑; mineral nutrient content ↑; LP ↓; activity of CAT, APX, GR ↑, but that of POD ↓	
					roots	LP ↓; activity of antioxidant enzymes (CAT, SOD, POD, APX, GR) ↑	

* ↑ indicates significant and ↑ ns indicates non-significant increase; while ↓ refers to significant decrease and ↓ ns to non-significant reduction.

sulfite reductase (SiR, EC 1.8.7.1), cyanoalanine synthase (CAS, EC 4.4.1.9) localized in cytoplasm and mitochondria and cytosolic Cys synthase (CS, EC 2.5.1.47) also produce hydrogen sulfide [2,4]. Recently, Corpas et al. [15] demonstrated the presence of H_2S in plant peroxisomes, too.

Like the other gasotransmitters NO or CO, hydrogen sulfide has proved to be an essential participant of several physiological processes (e.g. germination, lateral root formation, stomatal closure) at „normal circumstances". Li et al. [16] demonstrated that if *Jatropha curcas* seeds were pre-treated with Aminooxyacetic acid (AOA), an inhibitor of H_2S biosynthesis, endogenous H_2S content decreased and germination percentage was significantly lower than Control. The essential role of H_2S in lateral root emergence was also supported by a study [17] which showed an interaction among H_2S, NO and Ca^{2+} ions. Using the inhibitor of H_2S synthesis, Propargylglicine (PAG) and the scavanger of H_2S, Hypotaurine (HT) the number of lateral root primordia significantly reduced. It was also detected that the application of Sodium Nitroprusside (SNP) as NO donor enhanced the generation of endogenous H_2S, especially in lateral root primordia.

Some reports have already presented the signaling function of H_2S or the cooperation between H_2S and NO in regulating the stomatal apertures [18,19,9]. Nonetheless, H_2S also displayed to be important in delayed flower opening [20] and postharvest senescence of fruits through mediating the level of ROS and activating antioxidant enzymes [21,6].

Besides, supra-optimal levels of H_2S, mainly due to excess application of H_2S donors, might be toxic for plants. The typical symptoms of H_2S toxicity are lesions in leaves, retarded growth of plants (both shoot and root), decrement of chlorophyll content and consequently reduced photosynthetic efficiency [6,5]. Zhang et al. presented that toxic level of endogenous H_2S, deriving from high NaHS concentration (200μM<) may have inhibitory effect on primary root development *via* ROS overproduction.

Recent studies have confirmed the probable interaction among H_2S and Reactive Oxygen Species (ROS), Reactive Nitrogen Species (RNS) [9,22] resulting in modulation of nitro-oxidative status of the plant cells. H_2S itself is also regarded to be a member of Reactive Sulphur Species (RSS) [22] and beside Glutathione (GSH) and NO has an important role in posttranslational modification (namely persulfidation) of numerous proteins, as it was announced in case of *Arabidopsis* [23].

The Role of H_2S in Plants under HM Stress

Many researchers ascertained that the increased emission of HMs

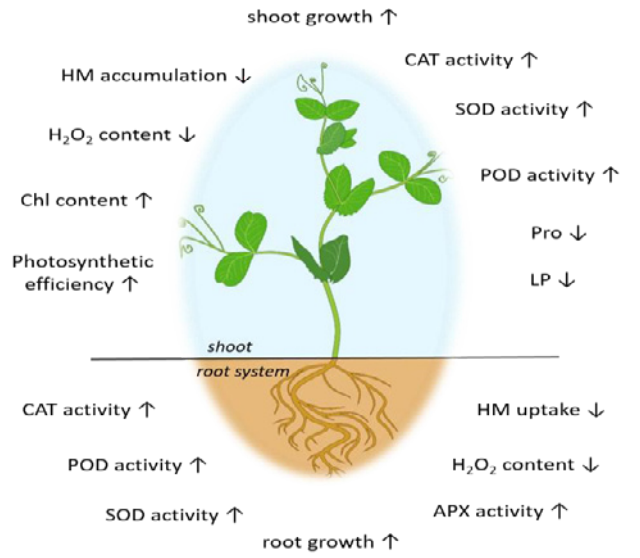

Figure 1: The effects of exogenous H_2S in HM stressed plants.

to environment originating from different sources like geological or anthropogenic activities (e.g. mining, industrial, excess application of fertilizers and pesticides or contaminated irrigation water) might have several negative effects on plants. The main symptoms of HM stress and/or toxicity in plants are generally disturbances in photosynthesis, reduced germination rate, abnormal development of vegetative parts (root and/or shoot) [24]. It is well-known that not only the toxic metals like Cd, Pb, Hg or As can cause nitro-oxidative stress in the plant cells but the essential HMs (e.g. Fe, Ni, Zn, or Cu) at supra-optimal concentration also cause ROS/RNS overproduction and consequently affect the activity of the antioxidant defense system [25,26].

There are some results demonstrating that HM stress irrespectively of being essential or non-essential can alter positively or negatively H_2S production in the plant organ investigated [27,28].

Beneficial Effects of Exogenous H_2S Treatment under HM Stress

Numerous studies have supported that the application of H_2S donors, like the most frequently used sodium hydrosulfide (NaHS) or the slow-releasing GYY4137 (morpholin-4-ium 4-methoxyphenyl(morpholino) phosphinodithioate) at a certain concentration may have significantly positive effects on seed germination [16,29, 14,30,31], lateral root formation [17], stomatal closure [18], as well as stress tolerance against salinity [32,33,12], heavy metals [34,35], drought [12,36], heat [37,38] and chilling [39,12] (Figure 1).

The results of the reports reviewed show that in plants HM stress is usually accompanied by nitro-oxidative burst which is realized in Lipid Peroxidation (LP), the accumulation of ROS/RNS and the activation of the antioxidant system, but generally it becomes well-balanced due to pre- or co-application of H_2S, both in root and shoot (Table 1).

NaHS pre- or co-treatment at various concentrations seemed to be advantageous for the plant in point of HM uptake by root and accumulation in shoot. Exogenous H_2S alleviated the uptake/accumulation of essential HM Zn in black nightshade [40, Table 1] or toxic HM Cd and Pb in rapeseed [34,35,41,28], Cr in barley [42] and *Arabidopsis* [43].

Since, aluminum (Al) is not a HM considering its density ($2.70gcm^{-3}$), but because of its toxic effects it is often regarded as HM [44], therefore we also take it into account. Exogenous H_2S also mitigated the uptake/accumulation of Al in rapeseed and barley [45,46, 58,59] (Table 1).

Moreover, the application of H_2S resulted in the increment Chlorophyll (Chl) and carotenoid content in the shoots (Table 1), as well, so it seems to have protective influence on HM stressed plants. The schematic model summarizes the main beneficial effects of exogenous H_2S treatment.

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