Plant in Challenging Environments 1

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Hydrogen Sulfide and Plant Acclimation to Abiotic Stresses

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Preface

Early studies on hydrogen sulfide (H_2S) exhibit its injurious effects on plants. However, over the last several years, H_2S has emerged as a potent regulator of plant growth and development. A vast number of physiological and biochemical processes are regulated by H_2S influencing plants at every stage of their life cycle. In plants, desulfuration of cysteine (Cys), by Cys desulfhydrases (CDes), synthesizes H_2S in various cell compartments. In addition, several other enzymes have been reported to synthesize H_2S in plants; however, L-Cys desulfhydrase 1 (DES1) has been recognized as the key enzyme involved in the generation of H_2S from Cys in the cytosol.

The existence of a dedicated system of H_2S synthesis, diffusion, sensing, and scavenging acknowledges the H_2S as a signaling molecule in plants. The signaling function of H_2S encompasses through its crosstalk with other signaling molecules like nitric oxide, carbon monoxide, abscisic acid, reactive oxygen and reactive nitrogen species, and calcium. Role of H_2S has been well investigated in mediating plant adaptive responses to a plethora of abiotic stresses such as drought, heat, cold, salinity, heavy metals, dark, and post-harvest stress. Also, the onset of these stresses induces endogenous synthesis of H_2S, which generates a downstream signaling cascade and mediates plant responses to the stressful conditions.

The initial signaling mechanism of H_2S is operated through post-translational modification of target proteins, a process known as persulfidation. In this process, reactive Cys residues on target proteins are modified via conversion of the thiol group into a persulfide group. Persulfidation is believed to play crucial role in the protective mechanisms against stress-induced impairments. However, the underlying molecular mechanism through which H_2S employs its action is not completely comprehended. Also, it has yet to be recognized the pathway(s) in which H_2S might be involved, and how and in what sequence H_2S functions in association with other signaling molecules.

Therefore, to expand our understanding of H_2S in plant biology under adverse conditions, the present book titled *Hydrogen Sulfide and Plant Acclimation to*

Abiotic Stresses was compiled. In this book, information on the biosynthesis of H_2S and its role in mediating plant responses to abiotic stress, mechanism of action of H_2S, its interaction with other signaling molecules, and their sequence of action in plants under various abiotic stresses is covered in the 12 chapters in an orderly manner.

The Chap. 1 deals with the various role of H_2S in plant physiological processes and its crosstalk with other molecules. Chapter 2 of this book presents a generalized view of H_2S functions in plants under various abiotic stresses. In Chap. 3, functional crosslinks of H_2S with other mediators in the formation of concrete adaptive reactions of plants, in particular, in the activation of antioxidative system, is discussed. Chapter 4 deals with the metabolism of H_2S and its protective role during metal toxicity in plants. Chapter 5 covers the role of H_2S in osmotic adjustment of plants under different abiotic stresses. Effect of H_2S on the accumulation of a range of plant osmolytes in response to the prevailing abiotic stresses was elaborated. Chapter 6 updates the readers with current knowledge on the role of H_2S in the signaling network that commands stomatal movement in response to external and endogenous stimuli. Chapter 7 presents an updated comprehensive overview of the H_2S metabolism and its implication in the ripening of climacteric and non-climacteric fruits. Additionally, the beneficial effects exerted by the exogenous application of H_2S during the ripening period and postharvest storage are also overviewed. Chapter 8 sheds light on the possible functions of H_2S during seed germination, with an emphasis on the mechanisms through which H_2S mitigates abiotic stress effects and maintains high germination efficiency under penalizing conditions. Chapter 9 provides the key roles of H_2S in plants under abiotic stresses such as metals, high salinity, drought, and extreme temperatures. The crosstalk among H_2S, phytohormones, second messengers, and metabolites is also addressed. In Chap. 10, the authors present a proteomic and transcriptomic overview of the mechanisms of H_2S signaling network involved in plant adaptive responses to abiotic stresses. Chapter 11 is focused on the significance of Cys in H_2S-mediated protective mechanisms and their interactive role in alleviating abiotic stress-induced impairments. Besides, the role of Cys and its allied molecules and products in the mechanisms responsible for plant acclimation to environmental stresses is also discussed. Chapter 12 sheds light on the role of H_2S in posttranslational modification of proteins and the importance of persulfidation in H_2S-meidated plant adaptive responses to abiotic stresses. Also, the methods for the detection of protein persulfidation are discussed.

The diversity of chapters presented in this book certainly expands the understanding of the readers. We hope the book will play a pivotal role in closing the gap of information and in opening new avenues in the field of H_2S research in plant biology.

We express our heartfelt gratitude to all the authors and reviewers of this book. We acknowledge the assistance from Dr. D. K. Gupta, Prof. J. M. Palma, and Prof. Francisco J. Corpas, editors of the book series Plant in Challenging Environments. Moreover, we are highly thankful to Springer Nature, Switzerland, and Ms. Zuzana Bernhart, Executive Editor Plant Sciences – Books, for the professional support and cooperation during the preparation of this volume.

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Contents

Chapter 1

Hydrogen Sulfide on the Crossroad of Regulation, Protection, Interaction and Signaling in Plant Systems Under Different Environmental Conditions

Zahid H. Siddiqui, Zahid K. Abbas, M. Wahid Ansari, and M. Nasir Khan

Abstract Due to climate change, the severity of the damage caused by the biotic and abiotic stress is unprecedented. In order to overcome the loss of productivity plant scientists are trying to elucidate the mechanisms of organism's response to environmental changes worldwide. Their findings recorded that the organisms make physiological adjustments and genetic changes to adapt in a new environment. These adjustments and changes require the participation of an array of signaling molecules like reactive oxygen species (ROS), reactive nitrogen species (RNS), carbon monoxide (CO), nitric oxide (NO), hydrogen sulfide (H_2S), calcium (Ca), salicylic acid, phospholipids etc. The understanding of how these molecules cross talk within the organism will elucidate the mechanisms through which they adapt to their external environment. Among these molecules, H_2S is on the crossroad of regulation of the processes at key cellular, sub-cellular, and molecular level in plants and known to play a vital role in plant growth and development. The signaling molecule H_2S, protects plants from various types of biotic and abiotic stresses. Moreover, H_2S also interacts with different phytohormones and other signaling molecules like Ca and NO in different metabolic processes in plants under different environmental conditions.

Keywords Abiotic stress · Autophagy · Climate change · Hydrogen sulfide · Photosynthesis · Signaling

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1.1 Introduction

In this era of climate change, every living organism on the planet Earth is experiencing stress in its life cycle. The stress falls into two categories, biotic and abiotic of both natural and anthropogenic origin, affecting the physiological metabolism, growth cycle, and epigenetic modifications of the organisms. Perhaps, the plants and other organisms have natural mechanism to overcome these stress factors but due to climate change, the severity of the damage caused by the stress is unprecedented. In order to get higher productivity from plants, researchers are trying to elucidate the mechanisms of organism's response to environmental changes worldwide. So far, it is well known that organisms adjust their physiology and genetic status to adapt in a changing environment (Kroll et al. 2014). Perhaps, these physiological and genetic changes require the participation of an array of signaling molecules like reactive oxygen species (ROS) (Ha et al. 2018), reactive nitrogen species (RNS) (Hancock et al. 2011; Zhang et al. 2018), carbon monoxide (CO) (Wareham et al. 2018), nitric oxide (NO) (Khan et al. 2017, 2020), calcium (Ca) (Dodd et al. 2010; Wang et al. 2016), salicylic acid (Guo et al. 2017), and phospholipids (Liu et al. 2017).

Similar to NO and CO, hydrogen sulfide (H_2S) is the third gasotransmitter, which is present in bacteria, plants, invertebrates, and vertebrates, including mammals, and control their physiological and biochemical activities (Hancock et al. 2011; Mancardi et al. 2009; Wang 2012). The understanding of these molecules and their cross talk within the system elucidate the mechanisms through which organisms adapt to their external environment. However, the H_2S is an enigmatic molecule but at the same time, it is one of the important compounds from Stanley Miller's spark discharge experiments for origin of life on Earth (Bada 2013), and has surplus functions in all forms of life. A few decades ago, H_2S was a gaseous pollutant, produced primarily by burning of fossil fuels. However, over the years several reports recognized its endogenous production as a signaling molecule. Being a foul, colorless gas its study was exceedingly difficult, however, the emission of H_2S in plants was discovered from squash, cucumber, cantaloupe, pumpkin, cotton, soybean, and corn using sulfur-specific flame photometric detector (Wilson et al. 1978). Due to small size and neutral nature of H_2S, it can easily move between the cells and does not require any transporters, through the hydrophobic cellular membranes (Mathai et al. 2009). The H_2S regulates numerous physiological processes in plants and known to play an important role in plant growth and development as well as in the protection of plants against various environmental stresses (Jin and Pei 2015; Jin et al. 2017; Khan et al. 2018). In animals, the role of H_2S as a signaling molecule is in details with its own limitations and open-end questions. The scenario in case of plant is quite different because of the late recognition of signaling role of H_2S in plants (Zhang et al. 2008a). Primarily, H_2S was known for its phytotoxic effects and its function in plant sulfur metabolism. Not long ago, new functions of this gas has been reported like as an alternative of sulfur source in plant nutrition, an instrument to manage excess sulfur in the system and most importantly its role in regulation

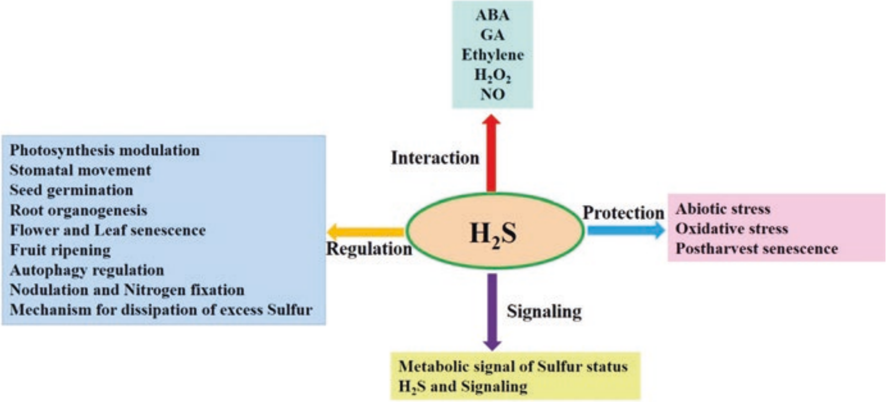

Fig. 1.1 Role of hydrogen sulfide (H_2S) in various processes of plant biology. *ABA* abscisic acid, *GA* gibberellic acid, H_2O_2 hydrogen peroxide, *NO* nitric oxide

and signaling (Lisjak et al. 2013; García-Mata and Lamattina 2013; Calderwood and Kopriva 2014). It acts as an important regulator of secondary messengers in different stress responses, plant developmental processes and activation of signal transduction cascades similar to NO (Zhang et al. 2008b; Shi et al. 2012; García-Mata and Lamattina 2013). Besides that, H_2S is a member of a crosstalk network which is shared with Ca, NO and abscisic acid (ABA) (Fotopoulos et al. 2015, Zhang et al. 2015a, b, Aroca et al. 2018). In this chapter, various roles of H_2S in plant systems and its crosstalk with other molecules will be explored (Fig. 1.1).

1.2 Biosynthesis and Role of H_2S in Plant System

Initially, H_2S was considered as a pollutant and a lethal gas for living organisms. In the plant system, biosynthesis of H_2S is predominantly occurring in chloroplast and to a lower extend in mitochondria and cytosol. Unlike animal system, in plants this process is controlled by multiple enzymatic systems, different from the sulfate assimilation pathway (Aroca et al. 2018). Mainly, following enzymes are responsible for the biosynthesis of H_2S in plants: L-cysteine desulfhydrase (LCD), D-cysteine desulfhydrase (DCD), β-cyanoalanine synthase (β-CAS), cysteine synthase (CS), sulfite reductase (SiR) and carbonic anhydrase (Rausch and Wachter 2005; Yamasaki and Cohen 2016). However, non-enzymatic pathway also contributes to the partial synthesis of H_2S as compared to the enzymatic pathway. In short, the process is overly complex and for further updated understanding the following reviews can be consulted (Calderwood and Kopriva 2014; Shivaraj et al. 2020). There are numerous reports that describe the phytotoxic effects of H_2S on plants (Rodriguez-Kabana et al. 1965; Lamers et al. 2013). In the report by Thompson and Kats (1978) high concentration of H_2S triggered injuries in the leaves, defoliation and reduced growth of the plants, however its low concentration was reported to be beneficial for the growth of Medicago, lettuce and sugar beet. Over the years, H_2S and plant -based studies have undergone in various directions and opened several avenues in plant biology (Fig. 1.1).

1.3 H_2S and Regulation of Physiological Processes in Plants

A vast array of literature is now available to confirm the role of H_2S in the regulation of various physiological/biochemical processes namely photosynthesis (Wang 2012; Chen et al. 2013), opening and closing of stomata (Papanatsiou et al. 2015; Jin et al. 2017; Chen et al. 2020; Shen et al. 2020), seed germination (Zhang et al. 2008a), root morphogenesis (Zhang et al. 2009; Jia et al. 2015; Mei et al. 2019), fruit ripening (Ge et al. 2017; Muñoz-Vargas et al. 2018), and senescence in leaves, flowers, and fruits (Zhang et al. 2011; Zheng et al. 2016). The role of H_2S during photosynthesis in *Spinacia oleracea* seedlings was studied in detail by Chen et al. (2011). Their results suggested that photosynthetic parameters such as maximum net photosynthetic rate (Pmax), maximal photochemical efficiency of photosystem II [F(v)/F(m)], carboxylation efficiency (CE), and the light saturation point (Lsp) reached to peak values under sodium hydrosulfide (NaHS) treatment. Besides that, the number of grana lamellae and activity of RuBisCO was significantly increased by NaHS treatment. Recently, Liu et al. (2019) reported that H_2S regulates photosynthesis of tall fescue under low-light stress. In their results the photosynthetic parameters, which are supposed to be reduced during low light conditions like net photosynthetic rate, chlorophyll content, photochemical efficiency of PSII, intercellular CO_2 concentration, enzymatic activity of RuBisCO etc., were significantly increased under NaHS treatment. Moreover, the antioxidant activities were enhanced by the NaHS treatment.

Plant system ensures its bulk and selective recycling, protection from pathogen and senescence by autophagy (Liu and Bassham 2012). Autophagy is a catabolic process in which consumption of the body's own tissues occurs in starvation or in diseases. In animals, the role of lysosomes and thier hydrolyzing enzymes are key factors in the process of autophagy. In plant system, the regulation of autophagy is associated with H_2S (Álvarez et al. 2010; Laureano-Marin et al. 2016). In starving Arabidopsis, H_2S prevents the ATG8 (autophagy-related ubiquitin-like protein) accumulation, thereby inhibits autophagy (Álvarez et al. 2012). This regulation was achieved by persulfidation of the enzymes involved in the autophagosome formation (Gotor et al. 2013). In Arabidopsis leaves, a high throughput proteomic approach reported persulfidation of some autophagy (ATG)-related proteins, ATG18a, ATG3, ATG5, and ATG7 (Aroca et al. 2017). Besides that, in yeast and algae, thioredoxin regulates ATG4 (Pérez-Pérez et al. 2014), in mammals ATG4b and ATG1 are controlled by phosphorylation and S-nitrosylation (Li et al. 2017; Pengo et al. 2017; Sanchez-Wandelmer et al. 2017), and Caspase-3, which is indispensable for autophagic activity, is persulfidated at Cys163 associating this amendment to the cytoprotective outcome of sulfide (Marutani et al. 2015). These reports suggest that persulfidation is the molecular mechanism through which sulfide regulates autophagy in Arabidopsis. Nevertheless, the recognition of other targets associated with autophagy needs additional detailed studies, and the constructive part of persulfidation in autophagy requires further investigation (Aroca et al. 2018).

1.4 H_2S and Protection of Plants Under Stress

As we discussed earlier, the adverse environmental conditions are responsible for negative growth, development, and loss of crop productivity. However, plants develop several mechanisms to overcome these adverse conditions. These mechanisms are regulated by generation of various types of ROS/RNS (Mantri et al. 2012). Further, new researches are suggesting the role of H_2S in response to adverse biotic and abiotic environmental conditions (Shi et al. 2015; Banerjee et al. 2018) along with a significant correlation between the functions of H_2S and NO (Corpas et al. 2019). The systematic understanding of the defensive mechanism of H_2S is relatively complex and challenging. The role of H_2S in plant protection from chilling stress (Fu et al. 2013), drought stress (Jin et al. 2017), osmotic stress (Khan et al. 2017), salt stress (Lai et al. 2014), and heavy metal stress (Guo et al. 2017; Khan et al. 2020) has been reported. The metal toxicity of copper, aluminum, chromium, cadmium, lead, arsenic, and zinc are effectively eased by H_2S (Zhang et al. 2008a; Chen et al. 2013; Mostofa et al. 2015; Liu et al. 2016; He et al. 2018, Khan et al. 2020). The role of exogenous H_2S in alleviating metal toxicity in plants is related to the concentration of H_2S supply (He et al. 2018). H_2S relieved the harmful effect of elements on plants by accumulating cell wall-related pectin methylesterase (PME), expansions, citrate, or plasma membrane (PM) H^+-ATPase (Wang et al. 2010; Chen et al. 2013). Recently, Corpas and Palma (2020) compiled the beneficial effects of the exogenous application of H_2S on a wide range of agricultural crops (rice, soybean, barley, wheat, maize, pea, cucumber etc.) affected by different kinds of abiotic stresses including heavy metals, salinity, drought as well as heat and cold stresses. Generally, the exogenous application of H_2S tends to increase the various components of antioxidant systems like catalase, ascorbate peroxidase, and superoxide dismutase which modulate the level of hydrogen peroxide (H_2O_2) and decrease lipid peroxidation. In *Brassica napus* the exogenous application of H_2S improved plant growth, root morphology, photosynthetic rate, and chlorophyll content. It also brings positive ultra-structural changes in the chloroplast (well-developed thylakoid membrane), mature Golgi bodies, mitochondria, and large endoplasmic reticulum in the root tip cells of *Brassica napus* (Ali et al. 2014). In alfalfa seedlings, H_2S enhanced Cd tolerance by regulating reduced (homo)-glutathione and ROS homeostasis (Cui et al. 2014). The protective role of H_2S against Cd in rice was managed by reducing oxidative stress and maintaining mineral homeostasis (Mostofa et al. 2015). He et al. (2018) proposed an action mechanism of H_2S-induced metal tolerance in plants. Perhaps in the initial step, H_2S regulates the metal transport proteins and thereby reduces the metal accumulation in the plants. It is followed by the improvement in the antioxidant capacity resulting in the scavenging of metal-induced ROS in plants by H_2S (Khan et al. 2020). In the final step, H_2S interacts with other signaling pathways, microRNAs (miRNAs) regulation and protein persulfidation under toxic metal stress. In banana fruit under low temperature, H_2S treatment can ease chilling injury by augmenting antioxidant system and the Δ^1-pyrroline-5-carboxylate synthetase activity which mainly attributed to an elevation in proline content (Luo et al. 2015).

1.5 H_2S Signaling and Interaction in Plants

The signaling molecule H_2S is involved in plant cross-adaptation, a known wild phenomenon of nature. There are evidences that suggest the signaling role of H_2S to activate downstream signal transductions and to reduce the heavy metals stress (Shi et al. 2014; Singh et al. 2020). If a plant is exposed to a mild stress, it can elicit the resistance to other stresses (Hossain et al. 2016). In case of winter rye, cold pretreatment can improve the heat tolerance, and UV-B can improve the heat tolerance in cucumber and the cold tolerance in *Rhododendron*. Similarly, mechanical stimulus can increase the heat tolerance and the chilling tolerance in tobacco cells (Knight 2000; Li and Gong 2013; Li et al. 2016). Furthermore, cross-adaptation can be induced between abiotic and biotic stresses (Foyer et al. 2016). In tomato, sunflower, pea, and rice infection by mycorrhizal fungi can increase the resistance to different abiotic stresses (Grover et al. 2011) and drought stress decreases the aphid fertility in *Arabidopsis* (Pineda et al. 2016). The intricacies of cross-adaptation are related to a complex of signal network that includes different secondary messengers like H_2O_2, NO, ABA, and Ca as well as their cross talk. The mild environmental stress or external use of signal molecules or their donors activate the cross-adaptation signaling, which in turn stimulates cross-adaptation by accumulating osmolytes, augmenting antioxidant system activity, producing heat shock proteins, as well as ameliorating ion and nutrient balance (Li et al. 2016).

There are reports that suggest that both H_2S and NO are involved in multiple pathways (Corpas et al. 2019b) and known to perform posttranslational modifications such as persulfidation and *S*-nitrosation, respectively (Aroca et al. 2018). The outcome of *S*-nitrosation regulates the role of different types of proteins and suggest the direct action of NO in various signaling processes. Similarly, the H_2S-assisted protein persulfidation provides protection against over-oxidation (Filipovic 2015; Aroca et al. 2018). The role of H_2S signaling is very promising in the regulation of stomatal movement. The stomata are the windows for gas exchange between plant and the atmosphere and H_2S is a gaseous molecule. Besides that, the NO signals stomatal closure with the help of ABA molecule is already reported (García-Mata and Lamattina 2001; Neill et al. 2002), but in another report García-Mata and Lamattina (2010) suggest the role of H_2S as a novel gasotransmitter involved in guard cell signaling. The H_2S induces stomatal closure and that inhibition of H_2S

production partially blocks the ABA effect on stomata. However, in another report, H_2S induces stomatal opening and reduces NO accumulation (Lisjak et al. 2010). In drought tolerance experiments, H_2S treatment induces closure of stomata (Jin et al. 2011; Shen et al. 2013). Jin et al. (2013) confirmed that by analyzing an *lcd* mutant with reduced H_2S accumulation; these mutants were more prone to drought stress and displayed increased stomatal opening in untreated mature leaves. The LCD gene encodes a PLP-binding protein with possible L-cysteine desulfhydrase activity, but in this line the T-DNA is inserted downstream the gene and disturbs the expression of another gene with unknown function. Therefore, it is not clear if LCD protein is another H_2S producing enzyme (Jin et al. 2013). Recently, Chen et al. (2020) reported that the enzyme SNF1-RELATED PROTEIN KINASE2.6 (SnRK2.6), which undergoes persulfidation, promotes ABA signaling and thereafter ABA-induced stomatal closure. Persulfidation-based modification of cysteine desulfhydrase and NADPH oxidase [Respiratory burst oxidase homolog protein D (RBOHD)] controls guard cell abscisic acid signaling (Shen et al. 2020). In light of these reports, the complete mechanism of action on stomatal aperture is still a long case, H_2S acts via regulation of ABC channels (García-Mata and Lamattina 2010), but the similarity in action of NO and H_2S cannot be ignored (García-Mata and Lamattina 2001). Further, it becomes more complex as H_2S interacts with ethylene to induce stomatal closure in *Arabidopsis thaliana* (Hou et al. 2013). In pepper plants, it is suggested that both NO and H_2S check catalase activity and supplement or antagonize each other in controlling H_2O_2 content by modulating the antioxidant enzymes (Kaya et al. 2020).

As compared to the association between H_2S and NO, the relationship between H_2S and H_2O_2 in plants is less understood. Recently, Liu et al. (2020) tried to reveal the mechanism underlying the interaction between H_2S and H_2O_2 in cucumber in response to photosynthesis. Their results suggest that H_2S and H_2O_2 increased the photosynthetic carbon assimilation, carbon metabolism, and photoprotection for both PSII and PSI in cucumber seedlings under chilling stress. They further suggest that H_2O_2 may act as a downstream signal in H_2S-induced protection as 1.0 mM NaHS considerably improved the relative gene expression of RBOH, which in turn contributes to raise the endogenous H_2O_2 accumulation in cucumber seedlings. However, H_2O_2 had little effect on gene expression of LCD/DCD and endogenous H_2S level (Liu et al. 2020). Further, in tomato seedlings H_2O_2 is involved in H_2S induced lateral root formation (Mei et al. 2017). In bermudagrass, exogenous application of H_2S improved Cd tolerance by modulating ROS and osmolytes together with NO (Shi et al. 2014) whereas, in case of arsenic, H_2S ease its toxic effects by up-regulation of ascorbate-glutathione cycle in pea seedlings with the involvement of NO that led to the reduced accumulation of arsenic (Singh et al. 2015). Also, in cucumber seedlings, H_2S relieve chilling damage by interacting with NO signaling (Wu et al. 2016).

1.6 Conclusion

Presence of H_2S in the cellular system initiates a signaling mechanism and induces different constituents of the antioxidant system at both the gene and protein level and protects the plants from abiotic stress, oxidative stress, and postharvest senescence. Further, H_2S regulates several physiological processes such as photosynthesis modulation, stomatal movement, seed germination, root organogenesis, etc. Besides, H_2S plays an active role in the transduction pathways of several other cellular signaling molecules including ABA, GA, ethylene, H_2O_2 and NO. Nowadays, H_2S is in focus to illuminate the crossroad of regulation, protection, interaction and signaling in various plant systems under different environmental conditions. However, the exact biochemical and molecular mechanisms to elucidate the role of H_2S in these processes still need more investigation. Therefore, the use of H_2S alone or combined with other molecules, such as NO, Ca, chitosan, thiourea, melatonin, and silicon, which seems to constructively improve crop productivity, should be explored in light of climate change.

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Chapter 2
Hydrogen Sulfide: A Road Ahead for Abiotic Stress Tolerance in Plants

Mehmet Tufan Oz and Fusun Eyidogan

Abstract Hydrogen sulfide (H_2S), a phytotoxic gas, is considered a signaling molecule at low concentrations with multiple physiological functions in plants during growth, development, germination, and response mechanisms to abiotic stress. Several reports have indicated that H_2S is released in plant cells as a crucial signal for the survival under different abiotic stress conditions. H_2S provides systemic resistance to different abiotic stress conditions mainly by reestablishing redox homeostasis, enhancing osmolyte accumulation, maintaining ion balance, and regulating gene expression. It also improves the plant tolerance to abiotic stress with its capacity to react with thiol groups. Like other gaseous signal molecules, H_2S is integrated in complex signaling networks with various second messengers such as calcium, hydrogen peroxide (H_2O_2), nitric oxide (NO), and abscisic acid (ABA). The objective of this review is to summarize the potential physiological functions of H_2S under various abiotic stresses.

Keywords Abiotic stress · Antioxidant system · Hydrogen sulfide · Redox homeostasis · Signalling molecules

2.1 Introduction

Changes in environmental conditions together with the climate change affect all ecosystems in the world. As a result of these changes, plants are faced with different stress factors which limit plant growth and productivity. Salinity, heavy metals (HMs), heat, drought, and other mechanical stresses are the most common

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environmental stress factors (Pandey et al. 2016; Zhang and Sonnewald 2017). When plants are exposed to abiotic stress factors, vital metabolic reactions are affected. These altered processes include osmotic and ionic imbalance and excessive accumulation of major reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), hydroxyl radicals (•OH) and superoxide ions ($O_2^{\bullet -}$) which induce irreversible cellular damage during these stress conditions. High concentrations of ROS in cells inhibit photosynthesis through stomatal closure and slow down key biochemical processes.

Plants develop different mechanisms to protect themselves from these unwanted stressful conditions. The protection mechanism starts with the perception of stress signal by receptors and that information is carried out by signaling pathways to generate a response in the cell. The main responses under stress conditions are the accumulation of organic solutes, both enzymatic and non-enzymatic antioxidants, and transcription factors (Pandey and Gautam 2020). However, timely and accurate perception of the stress signal and defense response to that signal, before the onset of stress-induced damage, is crucial for the endurance of plant under stressful conditions.

Priming of the plants with various chemical compounds has been found a promising way to enhance the stress tolerance mechanism in various plant species. After priming with a specific chemical or biological agent, plant defense system is activated under stress conditions. Among the priming agents, H_2O_2, polyamines, and nitric oxide (NO) occupy a prominent position that enhance stress tolerance in plants. Similarly, hydrogen sulfide (H_2S), another endogenous gaseous transmitter, is formed under various stresses and is found to be one of the effective priming agents. In addition, H_2S is a lipophilic molecule and is accepted as the third gas transmitter after NO and carbon monoxide (CO) (Wang 2002). In the late 1990s researchers showed that H_2S might have important functions in humans (Kimura 2015). In mammalian cells, H_2S was indicated as a possible signaling component in cells (Abe and Kimura 1996). Later, it was shown that H_2S is also produced by bacteria and plants where it functions as a signaling molecule (Da-Silva and Modolo 2018). Plants synthesize H_2S endogenously both in normal and stress conditions. The crosstalk between signaling pathways and H_2S indicates the role of H_2S in tolerance to different abiotic stresses (Niu and Liao 2016). Other studies showed that H_2S may have roles in antioxidant systems (Yu et al. 2013; Da-Silva et al. 2017), maintenance of K^+/Na^+ ratio (Lai et al. 2014; Deng et al. 2016), and osmolyte accumulation (Shi et al. 2013) under stress conditions.

Analysis of the effect of H_2S on different physiological processes in cells led to the use of potential donors of H_2S such as (*p*-methoxyphenyl)morpholinophosphinodithioic acid (GYY4137) and sodium hydrosulfide (NaHS). Exogenous application of a H_2S donor can improve tolerance to various abiotic stress in plants (Corpas and Palma 2020). Since plant genotype, concentration and duration of the treatment, and application methods affect plant behavior to H_2S, it is important to investigate endogenous dynamics of H_2S and potential effects of exogenous H_2S donors. The key role of H_2S in regulation of plant responses to unwanted environmental conditions in plants is given in Fig. 2.1.

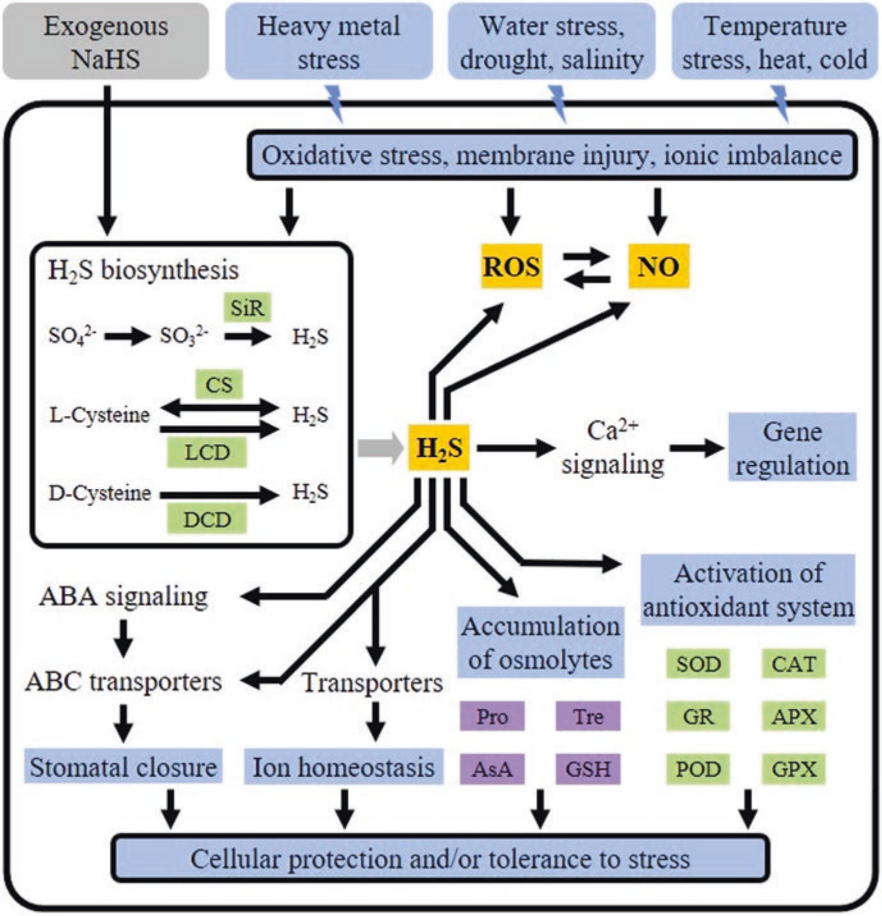

Fig. 2.1 Generalized illustration of key role of hydrogen sulfide in the regulation of response to environmental stress in plants. *ABA* abscisic acid, *ABC* ATP-bindind cassette, *APX* ascorbate peroxidase, *AsA* ascorbate, *CAT* catalase, *CS* cysteine synthase, *DCD* D-cysteine desulfhydrase, *GPX* glutathione peroxidase, *GR* glutathione reductase, *GSH* glutathione, *H_2S* hydrogen sulfide, *LCD* L-cysteine desulfhydrase, *NO* nitric oxide, *POD* peroxidase, *Pro* proline, *ROS* reactive oxygen species, *SiR* sulfite reductase, *SOD* superoxide dismutase, *Tre* trehalose

2.2 Biosynthesis of H_2S in Plants

The synthesis and emission of H_2S have been known long ago in corn, cucumber and soybean leaves (Wilson et al. 1978), and the enzymes involved in the biosynthesis of H_2S have also been identified (Riemenschneider et al. 2005). It was shown that compared to young plants, leaves from old plants contain higher H_2S levels (Rennenberg and Filner 1983). In plants, H_2S is mainly synthesized from L/D--cysteine or sulfide with enzymes including D-cysteine desulfhydrase (DCD),