

Invited Review

Hydrogen sulfide in plants: From dissipation of excess sulfur to signaling molecule



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ABSTRACT

Sulfur is essential in all organisms for the synthesis of amino acids cysteine and methionine and as an active component of numerous co-factors and prosthetic groups. However, only plants, algae, fungi, and some prokaryotes are capable of using the abundant inorganic source of sulfur, sulfate. Plants take sulfate up, reduce it, and assimilate into organic compounds with cysteine being the first product of the pathway and a donor of reduced sulfur for synthesis of other S-containing compounds. Cysteine is formed in a reaction between sulfide, derived from reduction of sulfite and an activated amino acid acceptor, *O*-acetylserine. Sulfide is thus an important intermediate in sulfur metabolism, but numerous other functions in plants has been revealed. Hydrogen sulfide can serve as an alternative source of sulfur for plants, which may be significant in anaerobic conditions of waterlogged soils. On the other hand, emissions of hydrogen sulfide have been detected from many plant species. Since the amount of H₂S discharged correlated with sulfate supply to the plants, the emissions were considered a mechanism for dissipation of excess sulfur. Significant hydrogen sulfide emissions were also observed in plants infected with pathogens, particularly with fungi. H₂S thus seems to be part of the widely discussed sulfur-induced-resistance/sulfur-enhanced-defense. Recently, however, more evidence has emerged for a role for H₂S in regulation and signaling. Sulfide stabilizes the cysteine synthase complex, increasing so the synthesis of its acceptor *O*-acetylserine. H₂S has been implicating in regulation of plant stress response, particularly draught stress. There are more and more examples of processes regulated by H₂S in plants being discovered, and hydrogen sulfide is emerging as an important signaling molecule, similar to its role in the animal and human world. How similar the functions, and homeostasis of H₂S are in these diverse organisms, however, remains to be elucidated.

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Introduction

The field of gaseous signal transmitters is relatively new in biology and rapidly expanding. The discovery of nitric oxide (NO) in animals and its function in cellular signaling has been a major breakthrough inspiring a whole new research field [1–3]. The area has been expanding in two directions; NO has been found to be important outside the animal kingdom, in plants [4,5] and yeast [6], and secondly, other gaseous signals have been discovered, namely carbon monoxide (CO) [7] and hydrogen sulfide (H₂S) [8]. In contrast to NO, whose effect on living organisms has been revealed only recently, CO and H₂S have been long known for their toxicity and their function in signaling is an exciting new development. Similar to NO, research on H₂S signaling has rapidly developed with a large number of highly significant contributions. The recent opening of the Nitric Oxide journal to research on H₂S [9] is a clear demonstration of the momentum in H₂S research, as is the increased interest in H₂S signaling in the plant research community [10,11].

In plants, NO has been recognized and investigated in detail solely for its roles in signaling. This indeed appears to be its only function in plants. The new signaling molecule, H₂S, however, is a compound long known to plant scientists, and interest in H₂S was initially driven by its phytotoxic effects and its function in plant sulfur metabolism. Over the years, new functions for this gas have been recognized; as a mechanism for dissipation of excess sulfur, an alternative S source in plant nutrition, and most recently in regulation and signaling. Several excellent reviews pointed out the various roles H₂S plays in plants and proposed that it may be an important signal, similar to NO [10,11]. Here we discuss these different functions of H₂S in plants, the evolution of our view on this important gas, and critically review recent literature describing the diverse positive effects of H₂S on plant growth and stress tolerance.

H₂S as an intermediate of assimilatory sulfate reduction

Sulfur is essential for all living organisms as a key constituent of the amino acids cysteine and methionine, as well as cofactors, polysaccharides, lipids and iron–sulfur clusters. Plants (along with fungi and prokaryotes) are the assimilators, which reduce and incorporate inorganic sulfur, which is almost entirely available as oxidized sulfate, into organic forms via the reductive sulfate assimilation pathway [12].

The first step of sulfur utilization by plants is, therefore, the uptake of inorganic sulfate by sulfate transporters. Once in the epidermis, sulfate is transferred to central cylinder via plasmodesmata between cells. However sulfate can leak into apoplast, which is also thought to be important in sulfur distribution. This is likely via an as yet unidentified passive transport mechanism driven by the outside-positive gradient of membrane potential at the plasma membrane. Once within a cell, sulfate is either stored in the vacuole, or metabolized immediately [12,13].

Using the energy of ATP hydrolysis, sulfate is activated to form adenosine 5'-phosphosulfate (APS) by adenylation. This reaction is catalysed by ATP sulfurylase (ATPS). The high-energy phosphate–sulfate mixed anhydride bond produced makes further enzymatic catalysis highly favourable, however it also makes the APS synthesis very unfavourable, with the equilibrium constant strongly favouring the reverse reaction. In plants, APS synthesis is driven forward by coupling it to hydrolysis of the pyrophosphate product, and rapidly removing APS. In contrast to animals, plants are able to reduce activated sulfate in the plastid to sulfite using APS reductase (APR). Sulfite is then further reduced to sulfide by ferredoxin dependent sulfite reductase (SiR), and sulfide is finally

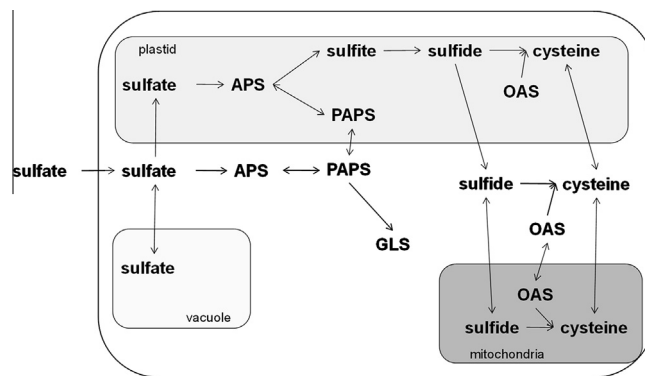


Fig. 1. Assimilatory sulfate reduction in plants. The scheme shows the localization of the individual reactions of sulfate assimilation. The activated sulfate, APS, represents a branch point between primary and secondary sulfur metabolism as it can also be phosphorylated by APS kinase (APK) to form 3'-phosphoadenosine 5'-phosphosulfate (PAPS), which acts as a donor of activated sulfate, and is involved in the modification of a variety of proteins, saccharides and secondary metabolites such as glucosinolates (GLS) [97].

incorporated into *O*-acetylserine (OAS) to form cysteine, the direct or indirect precursor of all organic compounds containing reduced sulfur in plants or animals. This is the assimilatory sulfate reduction pathway, (Fig. 1), by which sulfur enters primary metabolism, it is essential for survival, and cannot be compensated for by any other enzymatic process [12].

The sulfide formed by sulfite reductase is incorporated into OAS by *O*-acetylserine thiol lyase (OAS-TL) forming cysteine. OAS is itself synthesized from serine and acetyl-coenzyme-A by serine acetyltransferase (SAT) [14]. Under normal conditions cysteine synthesis is limited by OAS rather than sulfide levels as the concentration of OAS is found to be far below the K_m^{OAS} of OAS-TL isoforms, whereas sulfide concentration in the chloroplast and cytosol is higher than $K_m^{sulfide}$ [15]. Interestingly, whereas sulfide is produced exclusively in the plastids, cysteine synthesis takes place in all three proteogenic organelles. Three major OAS-TL and three major SAT isoforms are located in the plastid, cytosol and mitochondria [16–18]. Although each compartment is capable of producing sufficient cysteine to sustain growth, under normal conditions the bulk of the specific steps in cysteine synthesis are localized predominantly in different compartments. A coordinated interplay is necessary to assure that sulfide generated in plastids can react in the cytosol with OAS generated by mitochondria. The biological significance of this division of labor is, however, not known.

The ability of plants to grow with a single SAT or OAS-TL shows clearly that OAS, sulfide and cysteine are freely transferrable between compartments. For mitochondrial cysteine synthesis, sulfide is thus capable of moving across four membranes. It has been suggested that H₂S might diffuse across the chloroplast envelope [19], but the stroma of the chloroplast is at pH 8.5 under illumination [20], at which 95% of sulfide would be in the charged HS[−] form, and only poorly able to traverse lipid bilayers, therefore a protein transporter is likely. Such protein “bound” sulfide can be a direct substrate for OAS-TL and was part of a previously postulated “bound intermediate” pathway of sulfate assimilation [21], based on detection of intermediates of sulfate assimilation bound to proteins and a thiosulfonate reductase activity measured in algal extracts [22]. Whether free or bound, H₂S is an essential metabolite in plant cells and absolutely required for their survival. Knockdown mutant lines with reduced activity of sulfite reductase exhibit strongly retarded growth, and this enzyme is now considered to be a “bottleneck” in reductive sulfate assimilation that cannot be compensated for by any other enzymatic process [23]. However, probably because of this essential function, sulfite reductase is

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