Plant Science 241 (2015) 1–10

Contents lists available at ScienceDirect

Plant Science

journal homepage: www.elsevier.com/locate/plantsci

Review article

Plant sulfur and Big Data

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ARTICLE INFO

Article history:
Received 15 July 2015
Received in revised form 26 August 2015
Accepted 17 September 2015
Available online 21 September 2015

Keywords:
Sulfate assimilation
Systems biology
Genome wide association
Glucosinolates
Glutathione

ABSTRACT

Sulfur is an essential mineral nutrient for plants, therefore, the pathways of its uptake and assimilation have been extensively studied. Great progress has been made in elucidation of the individual genes and enzymes and their regulation. Sulfur assimilation has been intensively investigated by –omics technologies and has been target of several genome wide genetic approaches. This brought a significant step in our understanding of the regulation of the pathway and its integration in cellular metabolism. However, the large amount of information derived from other experiments not directly targeting sulfur has also brought new and exciting insights into processes affecting sulfur homeostasis. In this review we will integrate the findings of the targeted experiments with those that brought unintentional progress in sulfur research, and will discuss how to synthesize the large amount of information available in various repositories into a meaningful dissection of the regulation of a specific metabolic pathway. We then speculate how this might be used to further advance knowledge on control of sulfur metabolism and what are the main questions to be answered.

Contents

1. Introduction to sulfur research

Sulfur is an essential nutrient for all organisms due to its function in a large variety of processes. It is a vital component of proteins through the amino acids cysteine and methionine and an active constituent of numerous coenzymes and prosthetic groups, iron sulfur centres, coenzyme-A, thiamine, lipoic acid, *S*-adenosylmethionine, glutathione, and many more. Plant sulfur is also an important component of two major classes of natural products, the glucosinolates in *Brassicaceae* and alliins in *Allium* species. These secondary metabolites are not just defense compounds for the plants; they are the basis of smell and taste of cruciferous vegetables, garlic and onion and offer significant health benefits. These multiple roles of sulfur are mainly consequences of its ability to readily change its oxidation state [1].

Sulfur is abundant in nature, for example, the oceans contain 28 mM sulfate. The oxyanion sulfate is the major form of inorganic sulfur, which serves as a source for the biotic world, for aquatic

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Abbreviations: APS, adenosine 5′-phosphosulfate; GWAS, genome wide association study.

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http://dx.doi.org/10.1016/j.plantsci.2015.09.014
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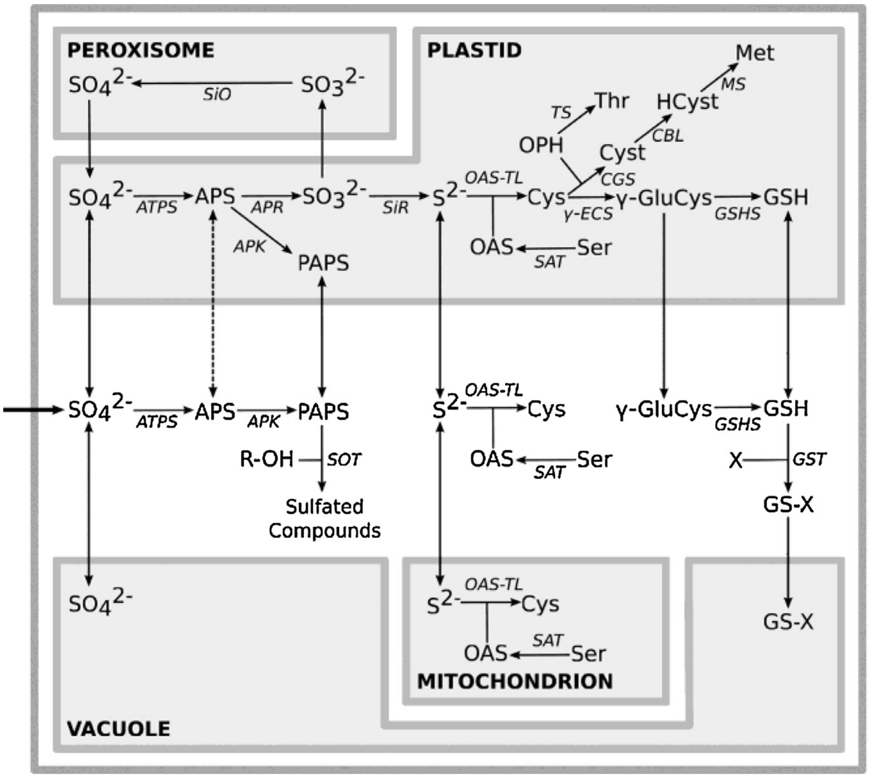

Fig. 1. Scheme of sulfate assimilation with compartmentation of the key steps. APS—adenosine 5′-phosphosulfate; PAPS—3í-phosphoadenosine 5′-phosphosulfate; OAS—*O*-acetylserine; OPH—O-phosphohomoserine; Cyst—cystathionine; HCyst—homocysteine; R—OH—hydroxylated acceptor of sulfate group; GS-X—glutathione conjugated with compound X; SiO—sulfite oxidase; ATPS—ATP sulfurylase; APR—APS reductase; APK—APS kinase; SiR—sulfite reductase; OAS-TL—OAS thiollyase; SAT—serine acetyltransferase; γ-ECS—γ-glutamylcysteine synthetase; GSHS—glutathione synthetase; CGS—cystathionine γ-synthase; CBL—cystathionine β-lyase; MS—methionine synthase; TS—threonine synthase; SOT—sulfotransferase; GST—glutathione S-transferase. Modified from [85].

as well as terrestrial organisms. However, most metabolites contain reduced sulfur as organic sulfide. Consequently, to use the abundant sulfate, organisms must invest energy into its reduction. Sulfate assimilation is, therefore, not an ubiquitous pathway. Metazoans and most parasitic bacteria do not reduce sulfate, and many bacterial and archae taxa specialize in oxidizing reduced forms of sulfur for energy production [2]. Sulfate uptake and assimilation are essential parts of plant primary metabolism. Plants serve as a source of reduced sulfur for animal and human nutrition.

1.1. *Sulfate metabolism*

Sulfate (SO_4^{2-}) is taken up and distributed throughout plant tissues by sulfate transporters, a family of membrane proteins differing in localization and affinity to sulfate [3]. The transporters are therefore divided into 4 distinct groups. High affinity sulfate transporters of group 1 in the roots are responsible for entry of sulfate into the plant. Low affinity group 2 transporters enable the loading and unloading of sulfate to and from xylem and phloem. Group 3 transporters transport sulfate through plastid membranes and enable its reduction. Transporters of group 4 are localized in the tonoplast and facilitate export of stored sulfate from the vacuoles. Altogether, plants contain 10–16 transporters. Some species also contain specialized transporters, e.g. for transport of sulfate into legume nodules (SST1 in *Lotus*) or in mycorrhiza symbiosis [1]. Green algae and many eukaryotic microalgae additionally possess a sodium-sulfate/carboxylate co-transporter family shared with animals and bacterial-like ABC transporters in plastid envelopes. These have been retained even in some basal plants such as the liverwort *Marchantia*. Sulfate influx into the vacuole is the last major flux of sulfate for which the corresponding transporter has not yet been identified [3].

Once sulfate enters the cell, it can be stored in the vacuole or directly enter the assimilation pathway. Plants can incorporate sulfate into bioorganic molecules either after reduction to sulfide, or in the oxidized form through sulfation reactions (Fig. 1). The former pathway has traditionally been called primary sulfate assimilation, whereas the pathway leading to sulfated metabolites is the secondary pathway [4]. Both pathways share a common intermediate, adenosine 5′-phosphosulfate (APS) produced from sulfate and ATP by ATP sulfurylase. APS can be reduced by APS reductase to sulfite (SO_3^{2-}), which is subsequently reduced to sulfide (S^{2-}) by sulfite reductase. Sulfide is incorporated into the amino acid skeleton of *O*-acetylserine to form cysteine, the first product of primary sulfate assimilation. Cysteine is the source of reduced sulfur for synthesis of methionine and all other metabolites containing reduced sulfur. Alternatively, APS can be phosphorylated by APS kinase to 3í-phosphoadenosine 5′-phosphosulfate, which serves as sulfate donor for the sulfation reactions in biosynthesis of a large range of metabolites, such as the peptide hormones phytosulfokines, brassinosteroids, sulfojasmonate, sulfoflavonoids, and the glucosinolates [1].

1.2. *Short history of research in regulation of sulfate assimilation*

Sulfate assimilation is under strict control. This is particularly important for the primary pathway, as the synthesis of cysteine merges assimilation of sulfate, nitrate, and carbon. These pathways must be coordinated. Sulfur containing compounds have numerous essential functions in the plant life cycle so that their synthesis must be maintained. However, the intermediates in sulfate reduction, sulfite and sulfide, are highly phytotoxic and their levels must be carefully controlled. Indeed, sulfate assimilation is tightly regulated according to demand. The pathway is down-regulated when plants