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Sulphur metabolism: The backbone of plant system

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Abstract
The sulphate (SO_4^{2-}) assimilation pathway provides the essential nutrient sulphur for plants with a tightly regulated and coordinated pathway with the demand for reduced sulphur (S). The responses of enzyme activities, mRNA levels and metabolite concentrations against numerous environmental cues and signals have been established for this pathway. In this review, different regulation mechanisms will be attended by identifying major gaps along with S-containing defence compounds (SDCs) in possible ways.

Keywords: sulphate, glutathione, sulphur, glucosinolates, OAS, ATPS.

1. Introduction
Sulphur (S) is the 4th macronutrient essential for growth and development of all the organisms. It is the main constituent of amino acids like cysteine (Cys) and methionine (Met), cofactors and prosthetic group like thiamine, Fe-S centers and S-Adenosyl methionine and a variety of primary and secondary metabolites. Sulphur metabolism in plants starts with the uptake of inorganic sulphate (SO_4^{2-}) from soil by sulphate transporters, its reduction into sulphide and finally incorporation into bioorganic compounds. In sulphate assimilation pathway, first activation of sulphate is carried out by ATP sulfurylase (ATPS) into adenosine 5-phosphosulfate (APS). The APS is a diverging point, which either can be phosphorylate by APS kinase into 3-phosphoadenosine 5-phosphosulfate (PAPS) or reduced by the activity of APS reductase into sulphite, which further is reduced by sulphite reductase (SiR) into sulphide followed by its incorporation into O-acetylserine (OAS) to make Cys, a donor of reduced S for all the metabolites. The PAPS is the donor of SO_4^{2-} for the sulphation of primary and secondary metabolites and peptides (Yarmolinsky *et al.*, 2013) [24]. The understanding about the molecular mechanism of regulation of sulphate assimilation is still lacking; therefore, in this review a summarized knowledge about the SO_4^{2-} assimilation mechanism will be discussed to identify the most significant gaps.

2. Sulphur sensing and signalling
The regulatory pathway is formed of sensors which detects the changes in the external and internal environment, signalling events which transmit information from sensors to the nucleus and triggers transcriptional response etc. But in higher plants the knowledge that how plant diagnose S deficiency, how plant get sensing for reduced S, or the sensing of refilled S pools. The two main theories exists to explain the sensing of S sufficiency/ deficiency, either the levels of downstream products of SO_4^{2-} assimilation or a receptor checking external (or apoplastic/vacuolar) SO_4^{2-}. There are two opinions indicating the SO_4^{2-} level monitoring by plants: the gene expression analysis in different mutants of S metabolism revealed that reduction in SO_4^{2-} content (*sultr1;2* and *fry1*) causes similar changes in gene expression as SO_4^{2-} deficiency even at normal SO_4^{2-} supply (Matthewman *et al.*, 2012) [13]. This hypothesis that SO_4^{2-} is the indicator of S status of plants was strongly supported after the new alleles of *sultr1; 2* (Zhang *et al.*, 2014) [25]. Under normal SO_4^{2-} condition, these mutants reveal a strong reduction in the levels of SO_4^{2-} and activate the genes involve in SO_4^{2-} limitation response, but when these mutants were kept in high SO_4^{2-} condition, the SO_4^{2-} level was restored in the mutants and the expression of SO_4^{2-} starvation marker genes stayed high which can be explained by claiming the extra function of SULTR1; 2 as sensor of SO_4^{2-} status (Zhang *et al.*, 2014) [25]. In green alga *Chlamydomonas*, a member of SO_4^{2-} transporter family SLC13 i.e. SAC1 SO_4^{2-} sensor was identified, which became useful in explaining the mechanism behind the SO_4^{2-} limitation response (Davies *et al.*, 1996) [4]. Therefore, it appears that SO_4^{2-} is useful in establishing the S status of plants but the role of Cys synthase complex cannot be neglected.

Besides SO_4^{2-}, different pathway intermediates like Cys, OAS, sugars, glutathione, ABA, cytokinins, jasmonate, ethylene, salicylate and nitric oxide affected by different metabolites. Some of these metabolites are considered as true signals like the role of cytokinins (under sufficient S availability), in suppressing the gene expression of SO_4^{2-} assimilation and similarly the role of these hormones in regulating the nitrate assimilation (Sakakibara *et al.,* 2006) [18], categorizes them a suitable candidates for signalling. However, one thing that should strike in mind is the role of OAS as signal is gaining controversies since decades. Generally OAS triggers the activities of APS reductase and SO_4^{2-} transporters (Koprivova *et al.,* 2000) [12]. Incubation with OAS induces gene expression including miR395 induction like that of SO_4^{2-} deficiency (Matthewman *et al.,* 2012) [13]. As OAS stores during SO_4^{2-} starvation, so logically it should considered as signal of SO_4^{2-} starvation, which further triggers the gene transcriptional changes; however, this is questioned that when the changes in gene expression in S starved plants actually lead to OAS accumulation, during time course of experiments (Hopkins *et al.,* 2005) [10].

The other signals which are essential in transmitting the signal of adequate levels of reduced S compounds are Cys, H_2S, and GSH. Since, these compounds are interconnected; hence one compound feeding results into increased levels of others so identification of real signals is very difficult. Among these, H_2S is specific one due to its gaso-transmitter nature, which is found protective against different environmental cues in plants (Sun *et al.,* 2013) [19]. GSH and Cys both induces gene expression i.e. suppress APS reductase and SO_4^{2-} transporters but as this effect can be weakened by inhibiting GSH synthesis by BSO, so GSH is more suitable candidate for signalling (Hartmann *et al.,* 2004) [9], which was confirmed by Ball *et al.* (2004) [1] by altering the gene expression in GSH synthesis mutants.

3. Profiles of sulphur-containing defence compounds (SDCs)

SDCs are significant in defence of plants against first infection, while pathogen-induced SDCs (S-rich protein (SRP) isoforms and phytoalexins) toughly participate in induced resistance. Though, the motto of SDCs designing was never to operate pathogen specific defence but they are expected to influence the specific gene-to-gene interactions between host and pathogen in due course of time.

3.1 Elemental sulphur

Recently, after studying the several plant species, elemental S (S_0) have been added to SDCs list, which is oldest fungicide most commonly used by plants for their defence (Williams and Cooper, 2004) [22]. Probably, GSH accumulation at specific sites followed by its degradation, leads to S_0 accumulation (Williams and Cooper, 2004) [22].

3.2 Glutathione (GSH)

GSH is the redox buffer, which accumulates in response to different stresses, protects different cellular organelle from reactive oxygen species (ROS) (Ruiz and Blumwald, 2002) [17]. In ascorbate-GSH cycle (AGC), the GSH functioning is interlinked with ascorbate (AsA) and electron flow from NADPH (Foyer and Noctor, 2005) [7]. In addition, it is also an essential part of glutathione-*S*-transferase (GST)-based detoxification mechanisms, synthesizes Cys-rich peptides using phytochelatin synthase (PCS), and a precursor of phytochelatins (PCs) (Dixon *et al.,* 2002) [5]. The possible mechanism behind the GSH achievements in defence against pathogen could be its ability in determining the redox status of NPR1 (nonexpressor of PR genes) proteins, which indirectly interferes with the salicylic acid-induced genes encoding pathogen-related proteins (Dong *et al.,* 2004) [6]. NPR1 in non-induced plants is confined within cytosol, found aggregated with the crosslinking of intermolecular disulphide bridges; which upon infection reduced into monomeric form and translocated to nucleus. The NPR1 is thought to be activated by change in redox potential during infection.

3.3 Hydrogen sulphide (H_2S)

The belonging of H_2S to SDCs is still unclear. Earlier it was believed that H_2S is released from Cys through a reversible OAS (thiol) lyase (OAS-TL) reaction; but at present different types of desulphydrases enzyme have been identified (Riemenschneider *et al.,* 2005) [16]. The specific role of these enzymes is still unclear but the activity and expression of L-cysteine desulphydrase was induced upon pathogen attack, which suggests the role of H_2S in plant defence (Bloem *et al.,* 2004) [2]. H_2S in cell is found in equilibrium with HS^-; and the H_2S toxicity released from the host against pathogen will depend on: (i) the ability of the pathogen to metabolize H_2S and (ii) H_2S conc. at the pathogen attack site.

3.4 Glucosinolates

Glucosinolates of Brassicaceae, one of the S-containing secondary plant products known for their defence role, which are derived from amino acids and have atleast two S atoms, one originates from phosphoadenosine phosphosulfate and the other from Cys (Wittstock and Halkier, 2002) [23]. Met derived glucosinolates have an extra reduced S (Textor *et al.,* 2004) [20], and glucosinolate-thioglucosidase combination operates as a dual component during defence. Thioglucosidases upon contacting, converted glucosinolates in to volatile hydrolysis products (isothiocyanates, epithionitriles, thiocyanates, nitriles and oxazolidine-2-thiones); which are defence-active products known to suppress the microbial growth (Wittstock and Halkier, 2002) [23]. Glucosinolates have both positive and negative roles during interaction between herbivore insects and *Brassica* genotypes (Giamoustaris and Mithen, 1995) [8]; therefore, these are concluded as generalized type to protect against pathogen, while specialized type are not affected by these compounds.

3.5 S-rich proteins (SRPs)

The S-rich defensins and thionins structures are stabilized by intramolecular disulphide bridges (Bohlmann and Apel, 1991) [3]. The in vitro analysis reveals that these peptides are toxic to yeasts, Gram-positive bacteria, nematodes or insects and a wide range of fungi (Bohlmann and Apel, 1991) [3]. In transgenic plants, overexpression of SRPs upgraded the resistance for fungal attack thereby highlighting the necessity of these proteins in plant defence (Peschen *et al.,* 2004) [15].

3.6 Phytoalexins

Abiotic elicitors and pathogen attack triggers the production of camalexin and brassinin like S-containing phytoalexins (Kliebenstein, 2004) [11]. The biosynthesis of tryptophan derived camalexin, which is affected (or effect on the compounds inducing camalexin) in *Arabidopsis* mutant

showed the clear cut role of camalexin in defence against different pathogens (van Wees *et al.*, 2003) [21]. The variation in results for different pathogens, credited to (i) full activation of camalexin after cell interruption, which depends on the nature whether biotrophic or necrotrophic, of pathogen, (ii) some fungi have the capability for camalexin detoxification (Pedras and Ahiahonu, 2002) [14].

Concluding remarks

Obviously our understanding for molecular mechanisms of regulation of SO_4^{2-} assimilation has been improved, but in some cases this information is still patchy/ inadequate. As various signalling mechanism are known but we do not know that how molecules transmit the signal and the functioning of most of the SO_4^{2-} -starvation induced genes is unknown. Therefore, the deep knowledge of molecular concepts of S-nutrition-enhanced defence capacities of crop plants will not be only helpful in developing plant breeding program but also will helpful in improving the plant cultivation techniques in sustainable agriculture.

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