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Thylakoidal Pigment-Protein Complexes: Critical Requirement of Sulphur for Proper Assemblage and Photosynthesis in *Arabidopsis thaliana*

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Introduction

Sulphur represents the ninth and least abundant essential macronutrient in plants. One-fifteenth to the nitrogen in plant dry matter sulphur plays crucial roles in the catalytic or electrochemical functions of biomolecules in the cells [1]. It is found in amino acids (Cys and Met), oligopeptides (glutathione [GSH] and phytochelatins), vitamins and cofactors (biotin, thiamine, CoA, and S-adenosyl-Met), and a variety of secondary products [2,3]. The thiol (sulfhydryl) group of Cys in proteins maintains protein structure by forming disulfide bonds between two Cys residues via oxidation. Sulphur is involved in mitigation against oxidative stress through GSH, for detoxifying xenobiotics and also required in formation of phytochelatins. It forms secondary products required in defense and signalling for fundamental cellular functions [1,4] and is a very important criterion for metal tolerance [3].

Further, sulphur is an important component of Fe-S cluster which are cofactors of proteins that perform a number of biological roles, including electron transfer, redox and non-redox catalysis and regulation of gene expression within all living organisms including plants. In chloroplasts, Fe-S clusters play a key role in photosynthetic electron transport as well as nitrogen and sulphur assimilation. The capacity of the Fe atom in Fe-S clusters to reversibly take up an electron provides the required electron carrier capacity in these pathways [5]. Sulphur limitation may affect plant primary production and growth due to defects in photosynthesis and related factors. These defects might ultimately be closely linked to a poor organization of MPCs in thylakoidal membrane as reported earlier in case of iron-deficiency [6]. Disorganized MPCs also result into impaired frame-up of photosynthetic pigments.

Thylakoid membranes are the sub compartments in which primary reactions of photosynthesis occur. In these reactions, about 100 proteins are involved and are organized in four major multisubunit protein complexes: the PSI, PSII, ATP synthase complex and cytochrome b6/f (cyt b6/f) complex [7]. Proteomics of the thylakoid membrane is an excellent approach to establish the number and identity of the proteins in pigment-multiprotein complexes (MPCs), localized to this compartment and to study the impact of nutrients, including sulphur, on their organization and composition.

The present study was undertaken with the aims to investigate impact of S-deficiency on organizational composition of thylakoidal MPCs with a perspective of taking equimolar chlorophyll to load on BNP gels and assess the amount of MPCs fetched, and estimate changes occurred in pigment concentration and photosynthetic efficiency of *A. thaliana leaf.*

Experimental

Arabidopsis thaliana ecotype 'Columbia' (Col-0) were procured from National Research Centre for plant Biotechnology, IARI (Indian agricultural research institute, Pusa, New Delhi, India). The seeds were germinated as previously described [3]. The plants were transferred to soil culture (Soilrite®) and grown for ten days supplied with Hoagland solutions [8] with sulphur (+S) or without sulphur (–S) as sulfate salts. For the S-deficient Hoagland media, SO_4^{2-} containing salts were replaced by equimolar amount of Cl^- (of K^+, Mn^{2+}, Zn^{2+}, Cu^{2+}) salts. Experiments were done in five replicates.

Thylakoid Isolation and Blue-Native PAGE

A. thaliana leaves were washed with cold water and used for extraction of thylakoid membranes as described by Timperio et al. [9] and processed as described by D'Amici et al. [10]. BN-SDS-PAGE, image analysis, tryptic digestion of proteins, peptide sequencing and identification was done as described previously [6]. BNP gels were loaded with 50 µg Chl per well.

Photosynthetic Pigments and Rate of Photosynthesis

Changes in contents of chlorophylls (a, b and a+b) and rate of photosynthesis were studied as described previously [3].

Results and Discussion

When *A. thaliana* plants were subjected to S-deficiency for 10 days, no additional band on BNP gel was observed indicating that there was no fragmentation/detachment of any major part in MPCs compared to control. However, bands of every MPC showed alteration in their composition. Equal amount of chlorophyll was used as a criterion for sample estimation which showed that there was an increase of 33%, 17%, 13%, 56%, 25% and 61% in PSII super complexes, PSI core/PSII dimer, RubisCO, PSII monomer/ATP synthase, LHCII assembly/LHCII trimers and LHCII monomers, respectively which Indicates a huge depletion of pigments from MPCs. However, a 5% decrease was noted in PSI monomer/Cytb$_6$f showing a severe depletion of pigments to PSI, perhaps most drastic feature occurring in thylakoids under S-deficiency. In chlorophyll content, a reduction of 5%, 25% and 27% was noted in Chl a, Chl b and total Chl (a+b), respectively. When comparing the rate of photosynthesis, a decline of 44% was observed indicating a probable loss of Fe-S clusters which are essentially required for redox reactions (Balk and Pilon, 2011). Thus this study suggests that S-deficiency decreases the amount of photosynthetic pigments in MPCs besides clearly decreasing PSI monomer/Cytb$_6$f. A loss of the said pigments and major accumulation of LHCII monomer resulted into lower rate of photosynthesis and growth of plant (Figure 1 A-C).

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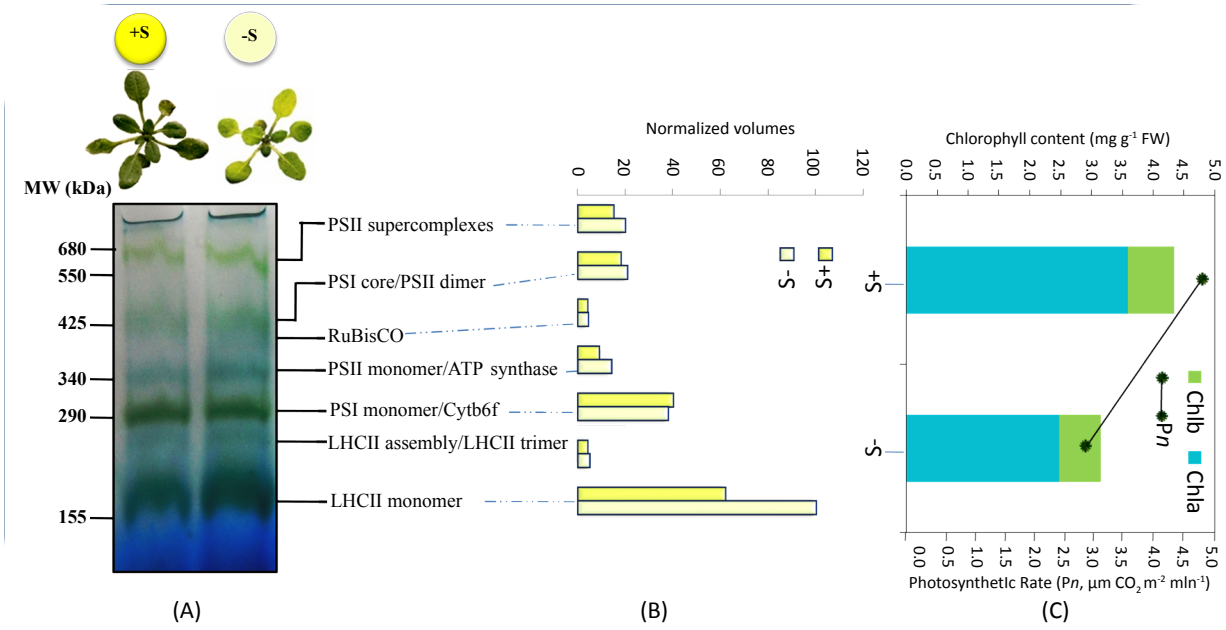

Figure 1: (A-C): *Arabidopsis thaliana* plants supplied with Sulfur (+S) were compared with plants kept deprived of S (–S) for ten days. (A) S-deficient (–S) plants showed pale color leaf which were also smaller in size. BN-PAGE showed the resolves MPCs of isolated thylakoids followed by, (B) A volumetric comparison of every protein complex based on the equimolar chlorophyll concentration and (C) Contents of chlorophylls (a, b and a+b) and rate of photosynthesis between +S (control) and –S plants.

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