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## PsbS DEPENDENCE IN LIPID AND PIGMENT COMPOSITION IN RICE PLANTS

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## PsbS-ЗАВИСИМЫЕ ИЗМЕНЕНИЯ В СОДЕРЖАНИИ ЛИПИДОВ И ФОТОСИНТЕТИЧЕСКИХ ПИГМЕНТОВ В РАСТЕНИЯХ РИСА

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*Abstract.* Plants acclimate to fluctuations in light conditions by adjusting their photosynthetic apparatus. When the light intensity exceeds, an unbalanced excitation of the two photosystems occurs. It results in reduced photosynthetic efficiency. Photosystem II (PSII) is the most susceptible and dynamically regulated part of the light reactions in the thylakoid membrane. Non-photochemical quenching of chlorophyll fluorescence (NPQ) is one of the short-term photoprotective mechanisms, which consist of the number of components. The strongest NPQ component — qE is localized in the PSII antenna and induced in plants by lumen acidification, the activation of the pH sensor PsbS, and the conversion of the violaxanthin to zeaxanthin within the xanthophyll cycle. Here, I present data that characterizes the role of the PsbS protein in organization of PSII structural components in isolated PSII-enriched membranes. The preparations were isolated from wild-type (WT) and PsbS-less (PsbS-KO) mutant rice plant. Based on the obtained results, the PSII-enriched membranes from WT and PsbS-KO differ as in the level of lipids, also in carotenoids. I conclude that the PsbS-dependent changes in membrane fluidity in PsbS-KO mutant plants compensated with increased lipid level in mutant plants.

*Аннотация.* Растения приспособляются к колебаниям освещенности, регулируя свой фотосинтетический аппарат. В условиях избытка света происходит несбалансированное возбуждение двух фотосистем, что приводит к снижению эффективности фотосинтеза. Фотосистема II (ФСII) — наиболее восприимчивая и динамически регулируемая часть световых реакций в тилакоидной мембране. Нефотохимическое тушение флуоресценции хлорофилла (NPQ) является одним из краткосрочных фотозащитных механизмов, которые состоят из ряда компонентов. Быстрый энергизационный компонент NPQ - qE локализуется в антенне ФСII и индуцируется у растений подкислением просвета тилакоидов, активацией белка ФСII PsbS, действующего как датчик pH и превращением виолаксантина в зеаксантин в рамках цикла ксантофилла. Здесь я представляю данные, характеризующие роль белка PsbS в организации структурных компонентов ФСII на изолированных мембранных фрагментах, обогащенных ФСII. Препараты выделены из растений риса дикого типа (WT) и мутантных растений, не содержащих белок PsbS (PsbS-KO). Исходя из полученных результатов, обогащенные ФСII мембраны WT и PsbS-KO различаются как по уровню липидов, так и по каротиноидам. Согласно полученным результатам PsbS-зависимые изменения текучести мембран у мутантных растений PsbS-KO компенсируются повышенным уровнем липидов в мутантных растениях.

**Keywords:** carotenoids, lipids, non-photochemical quenching, photosystem II, PsbS, rice, thylakoid membrane.

**Ключевые слова:** каротиноиды, липиды, нефотохимическое тушение, фотосистема II, PsbS, рис, тилакоидная мембрана.

### Introduction

Under natural conditions, land plants constantly undergo different biotic and abiotic stresses. One of the rapidly changing abiotic factors is light intensity. When the light intensity is exceeded, it causes photooxidative damage that destroys the photosynthetic apparatus of plants. When the excited chlorophyll molecules cannot transfer excitation energy to the pigments of the reaction center of photosystem (PS) II and convert it into oxygen, photooxidative damage occurs with excessive formation of reactive oxygen species (ROS) [1, 2]. Effect of the different light intensities on plants has investigated at the level of thylakoid membranes [3], genes [4, 5], proteins [6]. However, less known about the composition of plant metabolites.

Lipids are the main structural component, which is necessary for the functioning of the photosynthetic apparatus, also for different biological processes such as photoprotection, light harvesting, etc. They contribute significantly to plant abiotic stresses response mainly by maintaining the structure of chloroplasts and modifying membrane fluidity through regulating the degree of fatty acids desaturation. Lipid remodeling of photosynthetic membranes has become a vital function in the adaptation of plants to various adverse environmental conditions [7]. The thylakoid membrane of vascular plants mainly contains galactolipids, the most abundant among them are monogalactosyldiacylglycerol (MGDG, ~50% of total lipids), digalactosyldiacylglycerol (DGDG, ~25-30%), sulfoquinovosyl-diacylglycerol (SQDG, ~10-15%), and phosphatidylglycerol (PG, ~10-15%). MGDG, which exists in the membrane in a conical shape, predominantly forms non-bilayer phase, promoting membrane stacking [8], whereas DGDG, SQDG, and PG, cylindrically-shaped lipids, are proficient to assemble into bilayer (lamellar) structures [9]. Galactolipids play a specific role in thylakoid architectural reorganizations in response to high light (HL) stress and they contributing to thylakoid stacking [10]. The lipid composition of the thylakoid membrane influenced by the effect of various stress conditions such as temperature, water or salt stress, nitrogen deficiency, aluminum stress [11, 12]. The observed changes includes in chain length and the number of double bonds in fatty acids, as well as in the ratio between the two major lipids, MGDG and DGDG [13]. The lipid composition of the membrane is essential for the functioning of proteins [14], and it affects the light reactions of the photosynthesis. Thus, the functionality of plastoquinone (PQ) diffusion as an electron transporter can be modified by the thylakoid membrane lipid composition [15].

Carotenoids are also an essential component of all photosynthetic organisms, providing photoprotective and antioxidant properties. While the majority of carotenoids bound to specific sites of photosynthetic complexes, approximately 15% of the total carotenoid pool is freely dissipated in the lipid phase in *Arabidopsis* (*Arabidopsis thaliana*) chloroplasts [16]. Both carotenoids and lipids play a crucial role in PSI and PSII reaction centers. They are necessary for the non-photochemical quenching (NPQ), light-harvesting mechanisms, and protection against reactive oxygen species (ROS).

It is less known about how plants' metabolite composition responds to fluctuations in environmental conditions. Studies on mutant plants of *Arabidopsis* that lack PsbS (*npq4-1*) have shown reduced fitness under natural conditions in the field [17]. In contrast, plants overexpressing

PsbS (oePsbS) demonstrated an increase in triggering of the major, rapidly induced component of NPQ energy quenching (qE) [18, 19]. Because biosynthesis of chloroplast lipids is fine-tuned to thylakoid membrane remodeling during light acclimation [20], I investigated the metabolomics shift associated with lack of PsbS protein using PsbS knockout (PsbS-KO) mutant and wild type (WT) rice plants. While PsbS during NPQ induction promotes a reorganization of the photosynthetic membranes [21, 22], my main objectives were to observe whether the changes in pigment and lipid and composition of PSII enriched membranes depends on PsbS protein of PSII. Also, I investigated if the PsbS-dependent fluctuations in membrane fluidity influence the organization and abundance of the carotenoids and lipids.

### Results and Discussion

To analyze differences in the composition of lipids, I have used PSII-enriched membranes (BBY particles), extracted from rice WT and PsbS-KO mutant plant leaves. Total lipids were isolated from BBY particles and further analyzed by gas chromatography. Compared with WT, the amount of main lipids MGDG, DGDG, SQDG and PG increased significantly for the PsbS-KO mutants. While the total amount of lipids for WT was determined as a 252.9 nmol/g, but for PsbS-KO mutants, this number increased to a 354.8 nmol/g. In comparison with WT with an MGDG/DGDG ratio value of 1.6, this ratio increased to 1.8 in PsbS-KO mutant lines. The major increase I observed in the composition of MGDG with the amount of increased by 49% to a 195 nmol/g, whereas the minor increase by 27% to a 23 nmol/g was identified in the amount of PG. Less rise in compare with MGDG demonstrated in the amount of DGDG and SQDG by ~27% and 44%, respectively (Table).

Table

THE AMOUNT OF LIPIDS (NMOL/G.FR.WT) EXTRACTED FROM DARK ADAPTED BBY PARTICLES OF WILD-TYPE AND PsbS-KO MUTANT RICE LEAVES

Plant	Lipid classes	Concentration (nmol/g. fr. wt)	% of total
WT	MGDG	131.4±11.3	52
	DGDG	83.5±7.2	33
	PG	22.0±1.3	8.7
	SQDG	16.2±1.2	6.3
	TOTAL	252.9±23.7	100.0
PsbS-KO	MGDG	195.4±17.4	53.7
	DGDG	109.1±9.8	32.2
	PG	27.8±2.5	7.7
	SQDG	22.6±1.9	6.4
	TOTAL	354.8±32.3	100.0

As a next step, to investigate the changes in pigment compositions of PSII-enriched membranes (BBY) of WT and PsbS-KO mutants, we performed the pigment analysis of isolated BBY particles (Figure). The graph below demonstrates that the complex contained neoxanthin (Neo), violaxanthin (Vio), antheraxanthin (Anth), lutein (Lut), chlorophyll (Chl) b, Chl a and  $\beta$ -carotene. No zeaxanthin was detected in both WT and PsbS-KO samples, confirming that the complex was isolated from dark-adapted plant leaves. The pigment analysis of PSII enriched membranes showed that while the amount of Neo, Vio, Lut were higher in PsbS-KO mutant plants, but anth, Chl b and  $\beta$ -car showed higher results in WT samples. BBY preparations of PsbS-KO mutants associated with the slightly higher number of Neo in comparison with Wt. It has been reported by [23] that Neo and Vio are coordinately bound to LHCII, which is associated with the

xanthophyll cycle and the induction of the NPQ [24]. The excited-state quenching in LHCII correlates with Neo distortion [25]. Therefore, I suggest that the higher amount of the Neo and Vio in PsbS-KO mutant may be due to compensation of the absence of PsbS protein. The role of Lut in the charge-separation mechanism for excitation quenching in LHCII also was demonstrated [26]. I found no difference in amount of Chl a between WT and PsbS-KO mutant BBY preparations.

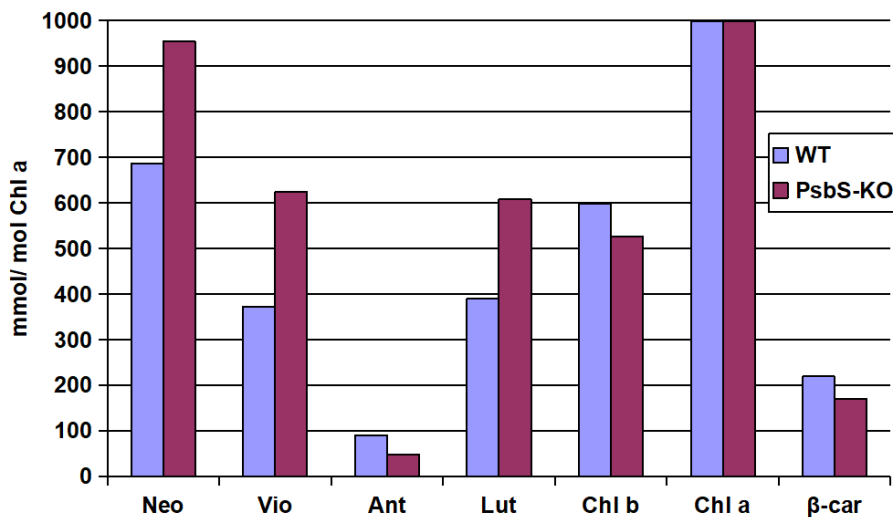


Figure. Composition of photosynthetic pigments in PSII-enriched membranes (BBY) of WT and PsbS-KO mutant lines

I found significant differences in lipid and pigment composition between the BBY preparations of WT and PsbS-KO rice leaves. It was earlier reported that under the influence of various stress factors, membrane restructuring is possible, where long-chain lipids are replaced by short-chain ones, and their saturation also increases [27]. Plants can rapidly modify previously accumulated lipids to compensate for the needs of the cell (for example, for fatty acids) under stressful conditions (changes in illumination, temperature, composition of the medium). The plants lacking PsbS induce a metabolic and transcriptomic shift that activates protective response mechanisms to increase resistance against biotic stress [12]. The synthesis of lipids is also apparently associated with the response cells to oxidative stress. So as the PsbS-KO mutant plants produce more ROS, I suggest that it results in enhanced synthesis of lipids and carotenoids. Also, the modulation of the membrane fluidity is directly associated with the composition of lipid-phase located carotenoids [16]. Following the previously published results [28, 29], I consider that the PsbS-dependent decrease in membrane fluidity in the bulk in thylakoid membranes of PsbS-KO mutant plants appears due to the lack of the PsbS protein and it compensated with the increased amount of lipids. Neoxanthin causes a largescale conformational change in the LHCII proteins [30], such unquenched LHCII intermediate with higher neoxanthin amount helps to understand the molecular mechanism of quenching. In this context, data obtained by me may indicate that LHCII in PsbS-KO plants might be under a quenching state.

### *Material and Method*

#### *Plants and growth conditions*

One-month-old seedlings of wild-type (WT) and PsbS-knockout mutant (PsbS-KO) rice (*Oryza sativa* L.) plants were grown in soil in a greenhouse under 30/26 °C (day/night), with a light photoperiod of 16 h of light/8 h of dark.

#### *Isolation of PSII enriched complexes (BBY)*

PSII complexes (BBY particles) isolated from WT and PsbS-KO mutant rice leaves as described by [31, 32] and then were stored at -80°C in a re-suspension medium containing 400 mM sucrose, 15 mM NaCl, 5 mM MgCl<sub>2</sub>, and 40 mM Mes (pH 6.5).

#### *Lipid analysis*

Total lipids extracted from PSII enriched membranes of two-week-old WT and PsbS-KO mutant plant leaves. Individual lipids were purified by one-dimensional thin layer chromatography as described by [12].

#### *Pigment analysis*

Pigments were extracted from PSII-enriched membranes (BBY) preparations of wild type (WT) and PsbS-KO mutant plants by gently agitating in ice-cold 100% acetone for 1 h. Samples centrifuged and the extracts filtered through a 0.2-µm syringe filter. The pigment composition of thylakoid membranes was determined by reversed-phase HPLC (HP 1100 series, Hewlett-Packard, Waldbronn, Germany) as described by [33].

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