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Complementary changes in absorption cross-sections of Photosystems I and II due to phosphorylation and Mg^{2+}-depletion in spinach thylakoids ☆

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Abstract

An open question regarding the changes of energy distribution between Photosystems (PS) I and II following protein phosphorylation and thylakoid destacking is whether or not excitation energy redirected from PS II antenna is effectively trapped by PS I reaction centers. In this report, we measured the effects in spinach thylakoids of Mg^{2+}-depletion and of phosphorylation at 5 and 1 mM $MgCl_2$ on: (1) the effective absorption cross-sections (σ) of both PS II and PS I determined simultaneously from single-turnover flash saturation curves of Chl *a* fluorescence and of the absorbance change at 820 nm, respectively; (2) the absolute changes in 77 K fluorescence yields emitted by PS II and PS I; and (3) the quenching of room temperature Chl *a* fluorescence. In all experiments, we observed complementary changes between $\sigma_{PS\ I}$ and $\sigma_{PS\ II}$, $\sigma_{PS\ I}$ consistently increasing at the expense of $\sigma_{PS\ II}$. ATP-induced decreases of $\sigma_{PS\ II}$ were 6.9% and 11.2% at 5 and 1 mM $MgCl_2$, respectively, whereas $\sigma_{PS\ I}$ increased by 12% and 18.6% under these conditions. In absence of Mg^{2+}, $\sigma_{PS\ II}$ and $\sigma_{PS\ I}$ changed respectively by −26.2% and +38.9% relative to thylakoids resuspended in presence of 5 mM $MgCl_2$. These relative increases of $\sigma_{PS\ I}$ are larger than the relative decreases of $\sigma_{PS\ II}$ by a factor of 1.5–1.7, probably due to the stoichiometry between PS II and PS I complexes typically found in sun-adapted spinach leaves. Also, we observed that the increases of $\sigma_{PS\ I}$ correspond closely to the increases of 77 K fluorescence yields emitted at 735 nm by PS I. However, no clear relationship could be detected between the changes of $\sigma_{PS\ II}$ and the quenching of both room temperature and 77 K PS II fluorescence. The reasons for such discrepancy are discussed.

Keywords: Antenna size; Photosynthetic unit; Pump-probe fluorescence method; State transition

1. Introduction

Trapping of absorbed light energy by the PS I and PS II complexes induces a transport of electrons through the thylakoid membranes of chloroplasts that provides the free energy required for the production of ATP and NADPH. Depending on prevailing environmental conditions and metabolic needs, some regulatory mechanisms contribute on different time scales to maximize the efficiency of photosynthetic energy conversion [1]. One of these mechanisms, the so-called state transitions, affects within minutes the distribution of excitation energy between the two photosystems and helps to maintain an equilibrium between their activities [2–4].

The key reaction leading to a redistribution of energy between PS II and PS I during state transitions is the phosphorylation of LHCII by a redox-controlled kinase activated under conditions known as state 2 [5]. In this state, the reduction rate of the plastoquinone pool by PS II exceeds its oxidation rate by PS I [6,7]. A fraction of phosphorylated LHCII reversibly dissociates from PS II and migrates toward non-appressed membranes enriched in PS I [7–9]. It is generally admitted that phosphorylation of LHCII causes a decrease of PS II cross-section, as judged from the similar decreases observed under in vivo conditions of the Chl *a* fluorescence parameters F_o and F_v and the decrease of 77 K fluorescence peaks at 685 and 695 nm emitted by PS II [5,6]. Reciprocal increases of 77 K fluorescence peak at 735 nm emitted by PS I indicate that

Abbreviations: F_{685}, F_{735}: 77 K Chl *a* fluorescence emitted at 685 nm and 735 nm, respectively; F_m, maximum yield of Chl *a* fluorescence when the PS II reaction centers are closed; F_o, minimum yield of Chl *a* fluorescence when the PS II reaction centers are open; F_v, $F_m - F_o$; $\sigma_{PS\ II}$ and $\sigma_{PS\ I}$: effective absorption cross-section of PS II and PS I.

☆ This paper is dedicated to Dr. David C. Fork on the occasion of his retirement.

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the excitation energy lost by PS II is redirected toward PS I [10,11]. However, the efficiency to which redirected PS II excitation energy is trapped by PS I reaction centers is still a matter of debate (see [5,12] for reviews). Complementary changes of PS II and PS I cross-sections during state transitions under both in vivo and in vitro conditions have been deduced from modulated fluorescence and photoacoustic experiments [13–15] and from the analysis of picosecond fluorescence decay components [16]. Small increases (12–15%) of the PS I cross-section were observed from light saturation curves of the extent of P700 photooxidation induced by single-turnover flashes [17,18] and from steady state P700 photooxidation rate measured under limiting irradiance [8]. On the other hand, no changes of the kinetics of Cyt *f* photooxidation [19] and P700 photooxidation [20] were found after LHCII phosphorylation. In membrane preparations containing only PS I complexes and LHCII, it was reported that phosphorylation of LHCII actually decreased energy transfer from LHCII to LHCI as seen by 77 K fluorescence excitation spectra and from an inhibition of PS I electron transport at sub-saturating light intensities [21].

Recently, Georgakopoulos and Argyroudi-Akoyunoglou [9] have observed that 'stroma lamellar' fractions isolated from phosphorylated pea thylakoids were enriched in LHCII but displayed a lowered 77 K F730/F685 fluorescence ratio. This indicates that the pool of LHCII found in these fractions after phosphorylation is not or poorly connected to PS I. In fact, these authors demonstrated that the enrichment of LHCII in the 'stroma lamellar' fractions isolated from phosphorylated thylakoid membranes results from a contamination by destacked peripheral regions of grana membranes. Therefore, it appears that phosphorylated LHCII do not migrate from granal to stromal membranes but rather toward the destacked outer regions of grana lamellae where they could interact with PS I complexes. Different extents of destacking could result in different degrees of interaction between phosphorylated LHCII and PS I in the grana margins, and therefore different alterations of the absorption cross-sections [9].

The extent of destacking of grana lamellae induced by LHCII phosphorylation is strongly dependent on the cation concentration in the assay medium [2,22]. At high cation concentrations, quenching of Chl *a* fluorescence resulting from LCHII phosphorylation does not affect the F_v/F_o ratio [23,24]. Such effects indicate that changes in the absorption cross-section are achieved by an alteration in the number of antenna complexes associated with PS II. At sub-saturating cation concentrations, preferential quenching of F_v after LHCII phosphorylation is consistent with the presence of direct energy transfer from PS II to PS I by spill-over [23,24]. However, it is important to note that other factors may contribute to changes of F_o and F_v during state transitions or Mg^{2+}-depletion and therefore complicate at least the quantitative interpretation of fluorescence quenching. Indeed, overestimation of the F_o level can result from the partial uncoupling between LHCII and PS II reaction center as observed at sub-saturating cation concentrations [25] and from the possible presence of uncoupled phosphorylated LHCII.

In this report, we measured in spinach thylakoids the effects of phosphorylation and thylakoid destacking on the effective absorption cross-sections of both PS II and PS I, which were determined simultaneously from the light saturation curves of the yield of Chl *a* fluorescence and from the extent of the absorbance change at 820 nm induced by single turnover flashes of various energies. We also recorded the absolute changes in 77 K fluorescence yields emitted by PS II and PS I as well as the quenching of room temperature Chl *a* fluorescence induced by phosphorylation and thylakoid destacking. This allowed us to relate quantitatively the changes of the fluorescence yield to the changes in PS II and PS I effective absorption cross-sections. Our results demonstrated that Mg^{2+}-depletion and phosphorylation of thylakoid proteins result in complementary changes of PS II and PS I effective absorption cross-sections indicating that redirected excitation energy from PS II was effectively trapped by PS I reaction centers under our experimental conditions.

2. Materials and methods

Thylakoids were isolated from fresh market spinach as described in [26] except that the resuspension medium consisted of 330 mM sorbitol, 30 mM Tricine/NaOH (pH 8.2), 10 mM KCl and 0, 1 or 5 mM $MgCl_2$ depending on experimental conditions. Chl $a+b$ concentration was measured as in [27].

Phosphorylated and non-phosphorylated thylakoid membranes were incubated for 30 min in the dark at a Chl $a+b$ concentration of 30 μM in presence of 5 mM Na dithionite, 10 mM NaF and in presence or absence respectively of 0.15 mM ATP. After that period, thylakoids were centrifuged and resuspended at a Chl $a+b$ of 10 μM in the same resuspension medium without ATP and Na dithionite.

PS II and PS I absorption cross-sections were determined respectively by flash saturation curves of Chl *a* fluorescence yield and of P700 photo-oxidation assayed by the extent of absorbance increase at 820 nm (Samson, unpublished results). The wavelength of the actinic laser pulses (250 ns duration), generated by a Phase-R DL-32 flash lamp pumped dye laser, was 650 nm. A small fraction of the actinic flash was directed toward a light pulse energy meter (Molectron) so that the energy of each laser pulse could be measured. 16 ΔA_{820}, fluorescence yield and flash energy signals were averaged simultaneously at a flash frequency of 0.17 Hz. Data were fit with the cumulative Poisson single hit probability distribution [12]:

$$\Phi(I) = \Phi_{max}(1 - e^{-I \cdot \sigma}) \quad (1)$$

where I is the pulse energy (photons/Å^2), $\Phi(I)$ is the yield of the photoproduct monitored, Φ_{max} is the maximal yield determined at saturating flash intensities, σ is the effective absorption cross-section (Å^2). For all determinations of σ values, 2 μM CCCP was added to the samples just before measurements. It has been shown that CCCP increases the yield of Chl *a* fluorescence from a single-turnover flash and decreases the extent of ΔA_{820} measured between 12 and 25 μs (Samson and Bruce, unpublished results). These effects were related to the diminution of P_{680}^+ concentration in the microsecond time range owing to the acceleration by CCCP of the reduction of oxidizing equivalents on the PS II donor side [28].

The absolute changes in the 77 K Chl *a* fluorescence yield emitted by PS II and PS I were recorded in a home-built spectrofluorometer described in [29]. Samples at a Chl $a + b$ concentration of 10 μM were transferred to 5 mm diameter glass NMR sample tubes and quickly frozen in liquid N_2. The absolute yield of fluorescence for each tube was determined from the average of 8 spectra taken after rotation of the tube by 45°. The excitation wavelength was 435 nm.

3. Results

3.1. Effects of phosphorylation

Dark incubation of spinach thylakoids under reducing conditions in presence of ATP results in the phosphorylation of several polypeptides, namely LHCII [22,30]. Changes of Chl *a* fluorescence yields resulting from such phosphorylation treatments done in presence of 1 and 5 mM $MgCl_2$ are presented in Table 1. Our experimental conditions rule out any artifacts caused by illumination such as fluorescence quenching related to photoinhibition. Room-temperature measurements showed that, although the F_o level was quenched to a similar extent (~ 10–12%) at both $MgCl_2$ concentrations, the F_v/F_m ratio decreased by only 1.7% at 5 mM $MgCl_2$, whereas it decreased by 21% at 1 mM $MgCl_2$. Fluorescence emission spectra recorded at 77 K exhibited opposite changes of the fluorescence yields emitted at 685 nm by PS II antenna and at 735 nm by PS I antenna. These changes, especially the quenching of F_{685}, were larger at 1 mM than at 5 mM $MgCl_2$. Similar effects of phosphorylation treatments on fluorescence yields were previously reported and interpreted as a redistribution of excitation energy from PS II toward PS I. At 5 mM $MgCl_2$, the results are consistent with the view of a pool of outer LHCII that dissociates from PS II complexes and migrates until it interacts with LHCI in non-appressed membranes. At 1 mM $MgCl_2$, the larger changes of Chl *a* fluorescence yields and the preferential quenching of F_v over F_o suggest that spill-over also contributes to energy transfer from PS II to PS I complexes (see [2,3] for reviews). However, those changes in

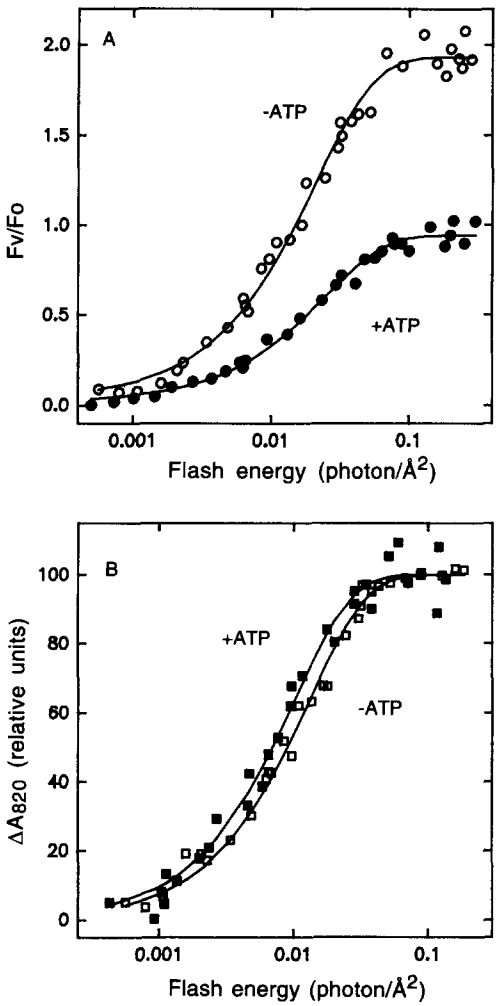

Fig. 1. Flash saturation curves of (A) the variable Chl *a* fluorescence F_v normalized to the F_o level and of (B) the relative extent of absorbance change at 820 nm (ΔA_{820}) measured from phosphorylated (closed symbols) and non-phosphorylated (open symbols) spinach thylakoids resuspended in the presence of 1 mM Mg^{2+}. The curves represent the fit of the experimental data to Eq. (1).

Table 1
ATP-induced changes of Chl *a* fluorescence parameters in spinach thylakoids resuspended in presence of 1 and 5 mM $MgCl_2$

	F_o	F_v/F_m	F_{685} (77 K)	F_{735} (77 K)
5 mM Mg^{2+}				
−ATP	2.11(0.06)	0.700(0.022)	67.5(9.8)	68.6(6.7)
+ATP	1.85(0.14)	0.688(0.021)	61.0(9.8)	77.6(5.7)
Δ	−12.3%	−1.71%	−9.6%	+13.1%
1 mM Mg^{2+}				
−ATP	2.27(0.08)	0.625(0.042)	54.8(6.3)	82.9(6.0)
+ATP	2.04(0.09)	0.494(0.017)	39.5(6.4)	100(−)
Δ	−10.1%	−21.0%	−27.9%	+20.6%

Parameters measured as described in Materials and methods. The results are the average of at least three independent experiments (S.D. in parentheses).

Table 2
Effective optical cross-sections of PS II and PS I ($\sigma_{PS\ II}$ and $\sigma_{PS\ I}$) estimated from single turnover flash saturation curves of variable fluorescence yield and ΔA_{820} in spinach thylakoids resuspended in presence of 1 and 5 mM $MgCl_2$

	5 mM $MgCl_2$		1 mM $MgCl_2$	
	σ_{PSII} (Å^2)	σ_{PSI} (Å^2)	σ_{PSII} (Å^2)	σ_{PSI} (Å^2)
−ATP	53.4 (6.3)	74.9 (10.9)	52.8 (5.9)	78.3 (1.7)
+ATP	49.7 (1.6)	83.9 (0.5)	46.9 (5.8)	92.8 (8.2)
Δ	−6.9%	+12.0%	−11.2%	+18.6%

fluorescence yields do not indicate to what extent redirected PS II energy is effectively trapped by the PS I reaction centers [21].

A more direct measurement of the effects of phosphorylation on energy distribution is the determination of effective absorption cross-sections σ for PS I and PS II from the light saturation curves of P700 photo-oxidation and Q_A reduction respectively. Fig. 1 presents the extents of ΔA_{820} and Chl *a* fluorescence yield as a function of photon density of single turnover flash measured simultaneously from phosphorylated and non-phosphorylated spinach thylakoids (Fig. 1). All curves fit closely the cumulative single-hit Poisson distribution (Eq. (1)). In thylakoids resuspended in the presence of 5 mM $MgCl_2$, the phosphorylation treatment resulted in a decrease of 6.9% of the $\sigma_{PS\ I}$ value, whereas $\sigma_{PS\ II}$ increased by 12%. At 1 mM $MgCl_2$, the changes in the effective absorption cross-sections were larger than at 5 mM $MgCl_2$ probably due to the presence of spill-over $\sigma_{PS\ II}$ decreasing by 11.2% and $\sigma_{PS\ I}$ increasing by 18.6%. The results are summarized in Table 2.

3.2. Effects of Mg^{2+}-depletion

Screening of negative charges at the surface of thylakoid membranes by cations is required to maintain the stacking of the granal membranes and the lateral segregation between PS II and PS I [31]. It is generally accepted that that the homogeneous distribution of the Chl protein complexes in thylakoid membranes resuspended at low cation concentration allows spill-over of excitons from PS II to PS I antennas [2,31,32]. Chl *a* fluorescence parameters and effective absorption cross-sections measured in thylakoid membranes resuspended in absence and presence of 5 mM $MgCl_2$ are presented in Table 3. Mg^{2+}-depletion has opposite effects on effective absorption cross-sections of PS II and PS I, $\sigma_{PS\ I}$ increasing (+38.7%) at the expense of $\sigma_{PS\ II}$ (−26.2%). These changes are closely correlated to the increase of the 77 K F_{735} (+39.7%) and the decrease of F_v/F_m ratio (−31.9%). Larger decreases (~ −43%) of F_m and 77 K F_{685} were observed, as expected from an increased rate of energy transfer from PS II to PS I antennas by spill-over [2]. In the absence of Mg^{2+}, we measured only a slight decrease of F_o (−1.9%), which is inconsistent with the observed change of $\sigma_{PS\ II}$. In fact, the expected F_o quenching was counteracted under our conditions by a significant increase of F_o level observed at sub-saturating (maximum at 0.5 mM) $MgCl_2$ concentrations (results not shown). Similar enhancements of F_o upon lowering cation concentrations were previously observed and attributed to a partial uncoupling of LHCII from the PS II reaction center [25,32]. Further cation depletion led to a F_o quenching by spill-over to a F_o level similar to the level observed at saturating cation concentrations.

4. Discussion

Distribution of excitation energy between PS I and PS II is largely influenced by the stacking of the PS-II-enriched granal membranes that allows lateral segregation between the two photosystems [7]. The formation of grana depends on the presence of LHCII that promotes adhesion between thylakoid membranes and on the presence of cations which neutralizes the repulsive forces of the negative charges at the membrane surface [33]. Increase of negative charge density at the level of LHCII after phosphorylation induces its dissociation from PS II complexes and causes partial destacking at the periphery of the grana [9]. The extent of this destacking is highly dependent on the cation concentration in the surrounding medium. At saturating cation concentration (e.g., 5 mM Mg^{2+}), phosphorylated LHCII uncoupled from PS II would migrate toward the non-appressed periphery of the grana and transfer energy to PS I whereas at sub-saturating concentrations (e.g., 1 mM Mg^{2+}), more pronounced destacking would also allow energy spill-over directly from PS II to PS I complexes (see [2]). Our measurements of ATP-induced Chl *a* fluorescence quenching characterized by a decrease

Table 3
Chl *a* fluorescence parameters and effective optical cross-sections of PS II and PS I ($\sigma_{PS\ II}$ and $\sigma_{PS\ I}$) measured in spinach thylakoids resuspended in the absence and presence (5 mM) of $MgCl_2$ estimated from light-saturation curves of variable fluorescence yield and ΔA_{820} induced from single turnover flashes

[Mg^{2+}]	F_o	F_v/F_m	F_{685} (77 K)	F_{735} (77 K)	σ_{PSII} (Å^2)	σ_{PSI} (Å^2)
5 mM	2.11 (0.06)	0.700 (0.022)	72.9 (4.1)	71.6 (3.7)	53.4 (6.3)	74.9 (10.9)
0 mM	2.07 (0.12)	0.477 (0.041)	40.6 (2.2)	100 (4.3)	39.4 (3.8)	104 (4.5)
Δ	−1.9%	−31.9%	−44.3%	+39.7%	−26.2%	+38.7%

of the F_v/F_m ratio at 1 mM but not at 5 mM $MgCl_2$, as well as the complementary changes of 77 K Chl *a* fluorescence yields emitted by PS I and PS II (Table 1), are in agreement with this view.

The ATP-induced changes of Chl *a* fluorescence yields do not solve the persistent problem regarding the extent of redirected PS II energy being effectively trapped by the PS I reaction centers [5,12]. Our simultaneous determinations of effective absorption cross-sections of PS I and PS II in phosphorylated thylakoids have demonstrated unambiguously that complementary changes occur between $\sigma_{PS\ I}$ and $\sigma_{PS\ II}$, where $\sigma_{PS\ I}$ increases at the expense of $\sigma_{PS\ II}$ (Table 2). At 5 mM $MgCl_2$, the ATP-induced changes of σ were small, especially for $\sigma_{PS\ II}$ (−6.9%), but consistent with previous reports. Falkowski and Fujita [34] found no statistical difference (with 10% variance) in the PS II cross-section from flash energy saturation curves of O_2 production and Chl *a* fluorescence of in vivo *Chlorella pyrenoidosa* cells adapted in state II compared to state I. From measurements of P700 photooxidation induced by single turnover flashes of different intensities, Telfer et al. [17] also found a 12% increase of $\sigma_{PS\ I}$ after phosphorylation treatment. Increases of the PS I antenna size following phosphorylation were also indicated by the enhancements of steady-state PS I electron transport rates measured at limiting light intensities (reviewed in [5]). Most of the controversy regarding the effects of phosphorylation on PS I antenna size comes from the absence of significant increases in the kinetics of P700 and Cyt *f* photooxidation under continuous illumination in phosphorylated thylakoids [19,20,35]. Under these conditions, the net photooxidation rate was measured since both photooxidation and re-reduction of P700 and Cyt *f* occur simultaneously. For valuable estimation of PS I absorption cross-section from photooxidation kinetics, the re-reduction rate needs to be taken into account [36]. The use of P700 photooxidation induced by single turnover flashes as in [17] and this study circumvents this problem.

The larger ATP-induced changes of absorption cross-sections observed at 1 mM relative to 5 mM $MgCl_2$ (Table 2), accompanied by a preferential quenching of F_v over F_o, is consistent with the presence of spill-over contributing to energy redistribution after LHCII phosphorylation at sub-saturating cation concentrations [23,24]. Clearly, effective energy spill-over from PS II to PS I complexes occurs after Mg^{2+}-depletion where $\sigma_{PS\ I}$ increases at the expense of $\sigma_{PS\ II}$ (Table 3). The observation that both flash saturation curves of ΔA_{820} and Chl *a* fluorescence in Mg^{2+}-depleted thylakoids fit closely the cumulative single hit Poisson distribution characteristic of a homogeneous population (Fig. 2) suggests that all the active photosynthetic units are affected to a similar extent by spill-over. Using different methods, Jennings [32] made similar conclusions. If spill-over involves virtually all LHCII-PS II complexes then the rate of exciton transfer from PS II to PS I by spill-over cannot exceed by a large factor the rate

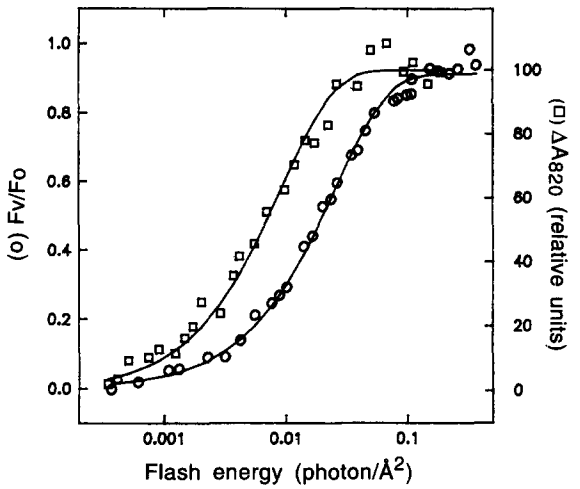

Fig. 2. Flash saturation curves of the variable Chl *a* fluorescence F_v normalized to the F_o level (circles) and of the relative extent of absorbance change at 820 nm (ΔA_{820}) (squares) in spinach thylakoids resuspended in the absence of Mg^{2+}. The curves represent the fit of the experimental data to the Eq. (1).

of exciton trapping by the PS II reaction center otherwise $\sigma_{PS\ II}$ would approach zero. Indeed, $\sigma_{PS\ II}$ decreased by only 26% upon Mg^{2+}-depletion.

Our parallel measurements of the Chl *a* fluorescence yields with effective absorption cross-sections indicates that $\sigma_{PS\ I}$ and 77 K F_{735} increased to the same extent after phosphorylation treatments at 1 and 5 mM $MgCl_2$ or following Mg^{2+}-depletion (Tables 1–3). A close relationship was previously reported between the quenching of room temperature fluorescence emitted by PS I core antenna complexes and the decrease of effective rate of P700 photo-oxidation under limiting light caused by the quenching of Chl excited states by 5-hydroxy naphtoquinone [37]. In contrast to $\sigma_{PS\ I}$, we found that no Chl *a* fluorescence parameter could reflect consistently the observed changes of $\sigma_{PS\ II}$. This is due to the presence of different mechanisms of energy transfer from PS II to PS I (spill-over and mobile phosphorylated LHCII) which quench to different extents the constant and variable parts of Chl *a* fluorescence [2,3]. Also, the relation between $\sigma_{PS\ II}$ and Chl *a* fluorescence is complicated by the origin of fluorescence quenching: decrease of $\sigma_{PS\ II}$ would result from quenching of excitation energy in the PS II pigment whereas fluorescence quenching owing to reactions happening within the reaction center of PS II would not affect $\sigma_{PS\ II}$ estimation [12,35].

Efficient redistribution of excitation energy between PS II and PS I should lead to complementary changes of $\sigma_{PS\ II}$ and $\sigma_{PS\ I}$. Interestingly, our results showed that the relative increases of PS I cross-sections induced by phosphorylation at 5 and 1 mM Mg^{2+} or due to Mg^{2+}-depletion were always larger by a factor of about 1.6 (from 1.5 to 1.7) compared to the relative decreases of PS II cross-sections. These relative changes are consistent with the PS II

to PS I ratio typically found in sun-adapted species like spinach, barley, and tobacco [38]. This also strengthens our conclusion that under our experimental conditions redirected energy from PS II antenna is efficiently used by the PS I reaction centers.

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