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MOVEMENT OF A SUB-POPULATION OF THE LIGHT HARVESTING COMPLEX (LHC_{II}) FROM GRANA TO STROMA LAMELLAE AS A CONSEQUENCE OF ITS PHOSPHORYLATION

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Phosphorylation in vitro of the light-harvesting chlorophyll *a*/*b* protein complex associated with Photosystem II (LHC_{II}) resulted in the lateral migration of a subpopulation of LHC_{II} from the grana to the stroma lamellae. This movement was characterized by a decrease in the chlorophyll *a*/*b* ratio and an increase in the 77 K fluorescence emission at 681 nm in the stroma lamellae following phosphorylation. Polyacrylamide gel electrophoresis indicated that the principal phosphoproteins under these conditions were polypeptides of 26–27 kDa. These polypeptides increased in relative amount in the stroma lamellae and decreased in the grana during phosphorylation. Pulse/chase experiments confirmed that the polypeptides were labelled in the grana and moved to the stroma lamellae in the subsequent chase period. A fraction at the phospho-LHC_{II}, however, was unable to move and remained associated with the grana fraction. LHC_{II} which moved out into the stroma lamellae effectively sensitized Photosystem I (PS I), since the ability to excite fluorescence emission at 735 nm (at 77 K) by chlorophyll *b* was increased following phosphorylation. These data support the 'mobile antenna' hypothesis proposed by Kyle, Staehelin and Arntzen (Arch. Biochem. Biophys. (1983) 222, 527–541) which states that the alterations in the excitation-energy distribution induced by LHC_{II} phosphorylation are, in part, due to the change in absorptive cross-section of PS II and PS I, resulting specifically from the movement of LHC_{II} antennae chlorophylls from the PS-II-enriched grana to the PS-I-enriched stroma lamellae.

Introduction

Chloroplast membranes of higher plants and green algae exhibit a marked spatial segregation of the pigment-protein complexes comprising two types of photochemical unit [1]. Photosystem II (PS II) is located primarily in the tightly appressed membrane regions of the grana, while Photosystem I (PS I) is thought to be in the non-apressed edge of the grana and in the stroma lamellae [2]. From thermodynamic arguments, Barber [3] has suggested that this phenomenon arises from a difference in the relative proportion of hydrophobic to electrostatic interactions in these two macromolecular pigment-protein complexes. In spite of both the lateral heterogeneity of the photosynthetic membrane and the fact that the absorption spectrum of PS II is slightly different from that of PS I [4], the two photosystems must operate in series to carry out noncyclic electron transport. Under varying environmental conditions, the pro-

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Abbreviations: Chl, chlorophyll; LHC_{II}, light-harvesting chlorophyll-protein complex of Photosystem II; PS I, II; Photosystem I, II; RC I, reaction center of Photosystem I; RC II, reaction center polypeptides of Photosystem II.

portion of excitation energy arriving at PS II and PS I will fluctuate. It should, therefore, be of significant adaptive advantage to control the distribution of absorbed excitation energy between the two photosystems under these fluctuating external conditions, or in response to the internal cellular and physiological demands of the system which may require the production of excess ATP (via cyclic PS-I activity), or excess NADPH which requires the tight coupling of PS I and PS II.

Recent ideas have suggested that the phosphorylation of certain pigment proteins (specifically the light-harvesting chlorophyll *a-b* complex serving PS II; designated as LHC_{II}), controls the distribution of excitation energy between PS II and PS I (Refs. 5–7, and review, Ref. 8). Kyle et al. [9] have proposed that a population of the LHC_{II} is able to move laterally from the PS-II-enriched appressed membranes to the PS-I-enriched stroma lamellae following protein phosphorylation. In this manuscript we present further evidence to support the 'mobile antennae' hypothesis for the control of the excitation-energy distribution in higher plants.

Materials and Methods

Thylakoid membranes were prepared from 21-day-old pea seedlings according to Kyle et al. [10] and resuspended to a concentration of 200 μg Chl/ml in 15 mM Tricine (pH 7.8)/0.1 M sorbitol/10 mM NaCl/5 mM $MgCl_2$/10 mM NaF. Phosphorylation of membrane proteins was carried out in the presence of 200 μM ATP in white light (200 $\mu E/m^2$ per s) as previously described [10]. For the preparation of labelled membranes, 10–20 μCi of [γ-^{32}P]-ATP (3000 Ci/mM) were included in the reaction mixture. Following phosphorylation, the membranes were immediately pelleted at 12000 × *g* for 30 s and resuspended to a concentration of 400 μg Chl/ml with the above resuspension buffer at 20°C. Recrystallized digitonin (1.75% in water) was added to the stirred membranes to give a final concentration of 0.4%. The 2 min detergent treatment was terminated by a 10-fold dilution of the sample with resuspension buffer at 0°C. Differential centrifugation according to Anderson and Boardman [11] yielded pellets following of 1000 × *g* for 10 min, 10000 × *g* for 30 min, 40000 × *g* for 30 min and 144000 × *g* for 60 min. In some cases the thylakoid membranes were sheared using a French pressure cell (4000 $lb/inch^2$) according to the method of Arntzen et al. [12], before differential centrifugation.

Electrophoresis of thylakoid membrane proteins was carried out in SDS according to Laemmli [13] at 6°C. In some cases, membranes were solubilized with an SDS/Chl ratio of 10 : 1 in order to visualize the undenatured chlorophyll-protein complexes after electrophoresis [14]. Chlorophyll-protein bands were excised from the gel and absorption spectra and 77 K fluorescence emission spectra analyses were used for identification. Some excised chlorophyll-protein bands were denatured by heating in SDS sample buffer (SDS/Chl of 20 : 1) and rerun according to Laemmli [13]. Fluorescence emission and excitation spectra at 77 K were obtained using an SLM Instruments scanning spectrofluorometer.

Results

To test the hypothesis that LHC_{II} moves from the grana to the stroma lamellae in response to its phosphorylation [9], stroma lamellae fractions (144000 × *g*) pellet) were prepared and the chlorophyll-protein complexes were visualized as green bands on polyacrylamide gels. If the 144000 × *g* fraction was prepared from a digitonin treatment of thylakoids, we could identify green bands corresponding to RC I (CP I), LHC_I [15], LHC_{II} and free pigment [11]. The fraction prepared from a French press treatment of thylakoids, however, did not have a green band corresponding to LHC_I but did have the Chl *a* and *b* containing LHC_{II} in an oligomeric form. Quantitation of the green bands with a gel scanner indicated that in both French press and digitonin preparations, a substantial increase in the LHC_{II} monomer green band could be seen following protein phosphorylation (Table I).

A decrease in the Chl *a/b* ratio in the stroma lamellae (144000 × *g* pellet) as a function of illumination time in the light with ATP (i.e., phosphorylating conditions) was observed (Fig. 1). Since no change occurred in the light if ATP was not present, the phenomenon was not simply a light effect. It is also apparent from Fig. 1 that this change in the Chl *a/b* ratio is completely reversi-

TABLE I

REDISTRIBUTION OF CHLOROPHYLL IN CHLOROPHYLL-PROTEIN COMPLEXES IN A STROMA LAMELLA FRACTION AS A CONSEQUENCE OF PROTEIN PHOSPHORYLATION

All values are given as the percentage of the total chlorophyll on the gel in the green band. A total of 10 μg chlorophyll were loaded in each lane. Samples were prepared either by the digitonin or French press methods outlined under Materials and Methods. CP I contained only Chl *a* and had a 77 K fluorescence maximum at 735 nm. LHC_{II} and the oligomer $(LHC_{II})_n$, contained a large Chl *b* absorption and had a 77 K fluorescence maximum at 680 nm. LHC_I contained a small but significant amount of Chl *b* and had a 77 K fluorescence at 730 nm. n.d., not detected; P, phosphorylated; NP nonphosphorylated.

Chlorophyll-protein complex	Digitonin			French Press		
	P	NP	P/NP	P	NP	P/NP
PS I (CP I)	47	53	0.89	56	70	0.80
$(LHC_{II})_n$	n.d.	n.d.	–	13	10	1.3
LHC_I	14	16	0.88	n.d.	n.d.	–
LHC_{II} (CP II)	17	4.2	4.1	12.3	2.2	5.6
Free pigment	22	27	0.81	19	13	1.5

ble in the dark. The kinetics of this change appear to follow very closely those reported for the phosphorylation of LHC_{II} [7]. We, therefore, conclude that Chlorophyll *b* is moving from the grana to the stroma lamellae concomitantly with the phosphorylation of LHC_{II}.

The polypeptide profiles of the grana (10 K pellet) and stroma lamellae (144 000 × *g* pellet) are shown in Fig. 2. The grana fraction is characterized by the major bands of the LHC_{II} (30 kDa holoprotein + 25–27 kDa apoprotein), the reaction center of PS II (RC II at 43 and 47 kDa)

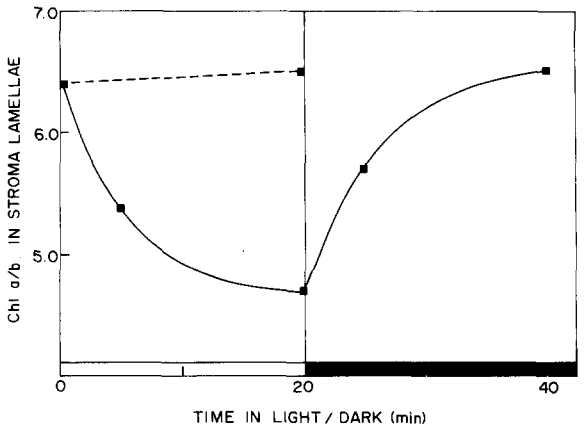

Fig. 1. Change in Chl *a*/*b* ratio in the stroma lamellae as a function of protein phosphorylation and dephosphorylation. Thylakoid membranes were incubated in the light for the first 20 min, then transferred to the dark for the remaining 20 min. Experiments were carried out in the presence of 200 μM ATP (solid line) or in its absence (dashed line).

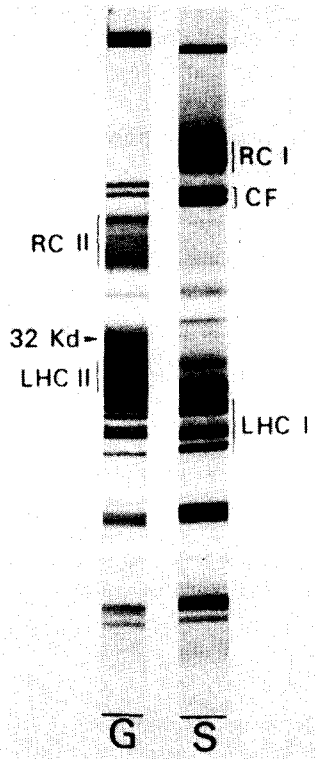

Fig. 2. SDS-polyacrylamide gels of the 10000 × *g* grana fraction (G) and the 144000 × *g* stroma lamella fraction (S). LHC I, light-harvesting components associated with PS I (as in ref 17) LHC II, light-harvesting complex associated with PS II.

and the Coomassie-staining PS II polypeptide at 32 kDa described by Kubarawa and Murata [16]. The stroma lamellae fraction is characterized by the reaction center of PS I (RC I at 68 kDa), the α and β subunits of coupling factor (58 and 56 kDa, respectively) and polypeptides in the range of 19–23 kDa which correspond to LHC_I according to Mullet et al. [17]. We have quantitated the relative amounts of Coomassie-staining associated with these polypeptides in phosphorylated and nonphosphorylated membranes by gel scanning. The results in Table II indicate little change in most of these components after phosphorylation with the notable exception of LHC_{II}. There appears to be a significant decrease of LHC_{II} in the grana fraction with a concomitant increase in the stroma lamellae following protein phosphorylation. This major increase in the stainable LHC_{II} in the stroma lamellae results in a proportional decrease in the other polypeptides, since equal amounts of chlorophyll were loaded in each lane. Of the total amount of LHC_{II} in the membrane, 88% is found in the grana and 12% in the stroma lamellae when membranes are nonphosphorylated (Table III). Following phosphorylation, however, approx. 15–17% of the grana-associated LHC_{II} moves out of the grana, effectively doubling the amount of LHC_{II} in the stroma lamellae. This is observed in electrophoretic profiles of heated samples (apoproteins only) and unheated samples (holoproteins + apoproteins).

Fluorescence spectra at 77 K provide information on the amount of light absorbed and reemitted from PS II and PS I. It has been previously demonstrated that phosphorylated membranes have an increased F_{735} signal (arising from PS I) relative to that at 695 nm (arising from PS II) in whole thylakoids [7]. This is also shown in Fig. 3a. Although the F_{735} is markedly reduced in the $10000 \times g$ fraction, phosphorylation has a major influence on increasing this component relative to F_{685} (Fig. 3b). Since LHC_{II} fluoresces at 685 nm [18], a decrease in the F_{685} relative to F_{735} may reflect loss of LHC_{II} from the grana fraction. The increase in the F_{735}/F_{685} in the grana following phosphorylation, therefore, is probably a result of both loss of LHC_{II} and an increase in spillover to what little PS I is present. The stroma lamellae fraction ($144000 \times g$ pellet) is made up almost entirely of the PS-I signal F_{735} (Fig. 3c). After normalization to this peak, it is apparent that a significant increase in a signal at 681 nm occurs following phosphorylation. This blue-shifted peak is characteristic of LHC_{II} which is not functionally attached to PS II [19,20].

Fluorescence excitation spectra of the F_{735} peak in whole thylakoids (Fig. 4a) indicates that there is an increase in the Chl *b* (480 nm) excitation of PS I in phosphorylated membranes. Since the majority of Chl *b* in thylakoids is associated with LHC_{II}, these data suggest that after phosphorylation LHC_{II} is acting as an atennae for PS I. This is more apparent in the excitation spectrum of F_{735} in the $144000 \times g$, stroma lamellae fraction (Fig.

TABLE II

DISTRIBUTION OF PROTEINS IN GRANA AND STROMA LAMELLA FRACTIONS BEFORE AND AFTER PHOSPHORYLATION

All values are given as the percentage of the total Coomassie staining proteins in each individual lane. Samples loaded onto the polyacrylamide gels were unheated; therefore RC I and LHC_{II} values are for the combined holoproteins and apoproteins. n.d., not detected; P, phosphorylated; NP, nonphosphorylated.

Component	M_r (kDa)	$10000 \times g$ Grana fraction			$144000 \times g$ Stroma lamellae fraction		
		P	NP	P/NP	P	NP	P/NP
RC I	68	7.6	7.7	0.99	25	29	0.86
CF ($\alpha+\beta$)	55+58	2.9	2.8	1.0	14	13	1.1
RC II	43+47	6.3	6.3	1.0	n.d.	n.d.	–
PS II component	32	8.0	8.0	1.0	n.d.	n.d.	–
LHC_{II}	25+30	36.0	42.0	0.86	14	5.9	2.4
LHC_I	19–23	8.6	8.4	1.0	15	22	0.71

TABLE III

DISTRIBUTION OF LHC_{II} BETWEEN GRANA AND STROMA LAMELLAE BEFORE AND AFTER PHOSPHORYLATION

Values were obtained from Coomassie stained bands as in Table II. Heated samples containing apoproteins only and unheated samples contained both apoproteins and holoproteins.

Treatment	Percentage LHC_{II} in grana		Percentage LHC_{II} in stroma lamellae	
	Heated	Unheated	Heated	Unheated
Nonphosphorylated	89	88	11	12
Phosphorylated	76	73	24	27

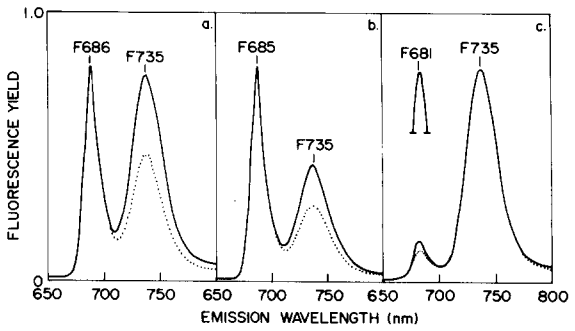

Fig. 3. Low-temperature (77 K) fluorescence emission spectra of chloroplast membranes (a), the 10000 × *g* grana fraction (b) and the 144000 × *g* stroma lamella fraction (c). Spectra are shown for phosphorylated (solid lines) and dephosphorylated (dotted lines) samples. Spectra in a and b have been normalized to 686 nm and those in c to 735 nm. Half-bandwidth resolution, 2 nm; ex, 440 nm.

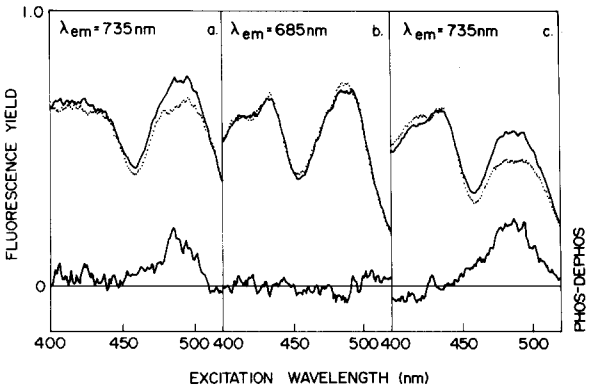

Fig. 4. Low temperature (77 K) fluorescence excitation spectra of chloroplast membranes (a), the 10000 × *g* grana fraction (b) and the 144000 × *g* stroma lamella fraction (c). Spectra are shown for phosphorylated (solid lines) and dephosphorylated (dotted lines) samples. All spectra have been normalized to the Chl *a* peak at 440 nm. The phosphorylated minus dephosphorylated difference spectra are shown below the individual spectra.

4c). In addition, there appears to be a minor loss of the Chl *b* contribution to the PS II signal (F_{685}) in the grana fraction in phosphorylated membranes (Fig. 4b).

The movement of Chl *b* and 25–30 kDa polypeptides from the grana to the stroma lamellae, and the appearance of an increased Chl *b* excitation to stroma lamellae PS I, indicate that LHC_{II} is moving from the grana to the stroma lamellae following phosphorylation. Direct evidence of this is given in the pulse/chase experiment shown in Fig. 5. Samples incubated with [^{32}P]ATP in the light for 20 min had most of the label in the grana fraction. This is not surprising, since 80–90% of the thylakoid LHC_{II} is isolated with the 10000 × *g* fraction. A 5 min incubation period in the light with [^{32}P]ATP also resulted in a much higher radioactivity in the grana relative to the stroma lamellae. If DCMU and NaF were added to the sample after 5 min of phosphorylation to prevent further phosphorylation or dephosphorylation, the amount of label in the grana decreased and that in the stroma lamellae increase over the subsequent 15 min chase period resulting in an approximately equal distribution of label between grana and stroma lamellae. Since 80–90% of the LHC_{II} is associated with the grana (Table III), we can conclude that the labelled LHC_{II} in the stroma lamellae had 4–9-times higher specific activity than the LHC_{II} of the grana in agreement with Andersson et al. [29]. We, therefore, propose that LHC_{II} is most likely phosphorylated in the grana and, once phosphorylated, a certain portion is free to move out into the stroma lamellae, where it can act as an antenna for PS I.

In order to determine which of the LHC_{II} polypeptides were being phosphorylated, we carried out SDS-polyacrylamide gel electrophoresis under nondenaturing conditions in order to retain green bands on the gel. The stroma lamellae fraction

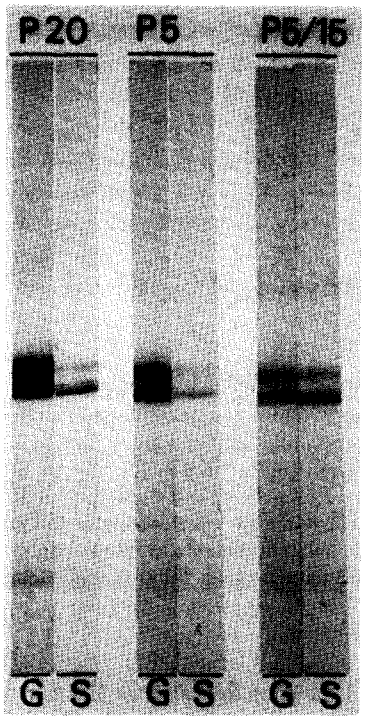

Fig. 5. Autoradiograms from SDS polyacrylamide gels of grana (G) and stroma lamella (S) fractions following phosphorylation with [γ-^{32}P]ATP. Fractions were prepared from membrane phosphorylated for 20 min (P20), 5 min (P5), and phosphorylated for 5 min followed by a 15 min chase (P5/15). The two labelled bands represent the undenatured holoprotein light harvesting complex (30 kDa) and the apoproteins of LHC at (26–27 kDa).

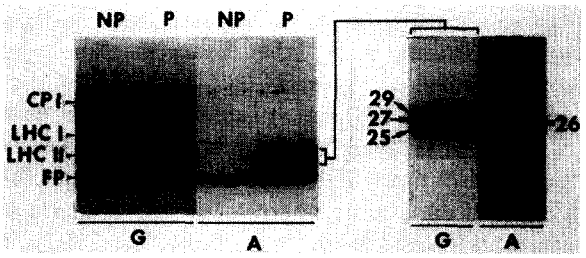

Fig. 6. Separation of chlorophyll protein complexes from the 144 K stroma lamella fraction by SDS-polyacrylamide gel electrophoresis. The unstained gel (G) and autoradiogram (A) are shown for both phosphorylated and nonphosphorylated samples. The labelled LHC II fraction was excised, denatured in SDS and rerun to give the gel pattern and autoradiogram shown. Numbers identify the apparent molecular weights. CP I, chlorophyll protein complex of photosystem I; LHC I, chlorophyll-protein complex associated with PS I; LHC II, chlorophyll-protein complex associated with PS II; FP, free pigment.

(144000 × g pellet) yielded green bands corresponding to those quantitated in Table I. Only the band corresponding to LHC_{II}, however, was labelled (Fig. 6a). When this labelled band was excised from the gel and rerun under denaturing conditions, the polypeptide profile in Fig. 6b was observed. It is evident from this gel that the major labelled polypeptide of the LHC_{II} was that migrating at 25 kDa, with a small amount of labelling occuring in the most heavily Coomassie-staining band at 27 kDa.

Discussion

Several lines of evidence indicate that the phosphorylation of LHC_{II} represents the in vivo control of the excitation energy distribution higher plants (review, Ref. 8). Until recently, however, the mechanism by which phospho-LHC_{II} could alter the amount of light energy arriving at PS I was not known. Barber presented the first explanation of how this mechanism might function based on analogies with cation-induced changes in excitation-energy distribution, and surmised that following phosphorylation, the PS II – LHC complex might move laterally into the stroma lamellae as is the case following membrane destacking [3,21,22]. A lack of a major destacking following protein phosphorylation [23–25] led us to question the proposal of Barber [21]; the hypothesis was specifically tested by freeze-fracture analysis of the chloroplast membrane during protein phosphorylation. Kyle et al. [9] presented direct evidence that a membrane subunit moved from grana to stroma lamellae concomitant with protein phosphorylation. They concluded that this particle was the LHC antenna only and not the PS II-LHC complex.

In this manuscript, we have tested the 'mobile antenna' hypothesis [8,9]. Six lines of evidence substantiate the concept. Following phosphorylation, (1) there is an increase in amount of the LHC_{II} Chl-protein complex as defined by SDS-polyacrylamide gel electrophoresis (CP II) in the stroma lamellae fraction; (2) the amount of Chl *b* (most of which is associated with LHC_{II}) increases in the stroma lamellae; (3) polypeptides in the region of 25–30 kDa (the LHC_{II} apoproteins) become depleted in the grana and enriched in the

stroma lamellae; (4) there is an increase in the 77 K chlorophyll fluorescence emission at 681 nm ('free' LHC_{II}) in the stroma lamellae; (5) there is an increased contribution of Chl *b* to the excitation of F_{735} in the stroma lamellae (LHC_{II} sensitization of PS I); and (6) pulse/chase experiments indicate pulse-labelled LHC_{II} movement from grana to stroma lamellae during the chase period.

The excitation spectra (Fig. 4) indicate that not only is the LHC_{II} moving into the stroma lamellae, but it is acting as an antenna for PS I. This confirms recent work demonstrating an increase in the quantum yield of PS I and a decrease in the quantum yield of PS II following protein phophorylation [7,26,27].

After 20 min of incubation under phosphorylating conditions, a major portion of labelled LHC_{II} remains in the grana (Fig. 5). Following a 15 min chase after 5 min phosphorylation, about half of the label remained in the grana. This suggests that there may be a certain population of LHC_{II} which is tightly fixed or immobilized in the grana, and a second population that is free to migrate laterally once phosphorylated. Armond et al. [28] reported that the large particles fracturing with the EF-face are most probably a composite of the PS II core and four surrounding LHC units, each of 80 Å diameter. In addition, Kyle et al. [9] reported that following protein phosphorylation, the EF particles did not decrease in size. Thus, the population of tightly fixed or immobile LHC_{II} may represent those units in tight connection with the PS II of the grana, and only the loosely attached population, that which fractures on the PF-face, is the mobile component.

Andersson et al. [29] have reported a 7-fold higher phosphorylation in the stroma lamellae LHC_{II} relative to the grana LHC_{II} on a chlorophyll basis. We interpret their data as indicating that the labelled LHC_{II} moved from the grana into the stroma lamellae, during the time between labelling of the LHC_{II} and the fractionation of the membranes. In our pulse/chase experiment (Fig. 5), almost equal amounts of radioactivity were present in the LHC_{II} of the grana and stroma lamellae (based on autoradiogram exposure densities). Since there is 4–5-times more LHC_{II} in the grana (Table II), we have a much higher specific activity in the LHC_{II} of the stroma lamellae, in agreement with Andersson et al. [29]. This is not the case, however, if the samples are fractionated immediately after 5 min phosphorylation or after prolonged labelling periods (Fig. 5).

It is apparent from Fig. 6b that two LHC_{II} apoproteins are labelled. This has also been reported by Bennett et al. [30] and by Andersson et al. [29]. Our data indicate that the smaller of the two apoproteins (26 kDa) is more highly labelled, as was also noted by Andersson et al. [29]. Bennett [30] reports an approximately equal distribution of counts with somewhat more labelling in the larger of the two polypeptides. The relevance of the differential labelling in the two apoproteins is not understood at this time, but may reflect a closer proximity of the 26 kDa component to the kinase.

In conclusion, we wish to stress the fact that there appears to be two populations of LHC_{II} in the thylakoid membrane; one which is tightly associated with PS II and unable to move following phosphorylation, and a second which is only loosely connected with PS II and, when phosphorylated, is free to migrate laterally out of the appressed regions of the grana into the stroma lamellae. The driving force for this type of movement is most likely an effect of the negatively charged phosphate on the balance between the repulsive electrostatic interactions at the membrane surface and the attractive Van der Waals forces in the hydrophobic region near the lipid bilayer as described by Barber [3]. Upon phosphorylation and movement into the unappressed membrane regions, the phospho-LHC_{II} is in much closer proximity to PS I and, therefore, can act as an antenna to PS I.

The movememnt of the phospho-LHC antenna from the grana to the stroma lamellae (the mobile antenna hypothesis) is a mechanism of control of excitation energy distribution which is significantly different than that induced by destacking [3] or by the lateral movememnt of a PS II-LHC complex as proposed by Barber [21–22]. Under certain conditions which may exist in vivo this latter mechanism might operate. However, we have been unable to find supporting evidence for the movement of a PS II-LHC complex following phosphorylation in vitro as hypothesized by Barber [21,22]. On the contrary, we have additional support for the mobile antenna hypothesis [8,9]. The

two concepts, however, need not be mutually exclusive. Based upon results of variable fluorescence at room temperature (Refs. 10 and 31; see also Telfer, A., Hodges, M. and Barber, J., unpublished data) and low temperature [32], it has been suggested that both a change in absorptive cross-section and 'spillover' occur as a result of protein phosphorylation. Indeed, a change of spillover has been observed in *Porphyridium*, an organism with neither LHC_{II}, nor lateral segregation of PS II and PS I [33,34]. It is, therefore, clear that although the 'mobile antenna' hypothesis can explain changes in absorptive cross-section, although details of the molecular mechanism by which 'spillover' is regulated remain incomplete.

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