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THE CATION-DEPENDENCE OF THE DEGREE OF PROTEIN PHOSPHORYLATION-INDUCED UNSTACKING OF PEA THYLAKOIDS

ALISON TELFER, MICHAEL HODGES, PAUL A. MILLNER and JAMES BARBER

AFRC Photosynthesis Research Group, Department of Pure and Applied Biology, Imperial College of Science and Technology, Prince Consort Road, London, SW7 2BB (U.K.)

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Experiments are presented to show that the phosphorylation of the light-harvesting chlorophyll *a*/*b*-protein complex (LHC) induces structural reorganisation within the thylakoid membrane in response to the introduction of additional negative surface charges. The effect of cations of different valency on chlorophyll fluorescence measurements indicates that LHC-phosphorylation-induced reorganisation involves a change in the electrostatic screening capability of the added cation. At intermediate levels of cations (e.g., 1 or 2 mM Mg^{2+}), which substantially stack non-phosphorylated membranes, it was found that membrane phosphorylation caused considerable unstacking as monitored by light scattering and electron microscopy. Concomitant with this was a large decrease in chlorophyll fluorescence indicative of randomisation of chlorophyll protein complexes which would result in an increase in energy transfer between the photosystems as well as an absorption cross-section change. At higher concentrations (e.g., above 5 mM Mg^{2+}) a persistent ATP-induced decrease in chlorophyll fluorescence has been attributed to the displacement of charged phosphorylated LHC from the appressed granal to the non-appressed stromal lamellae, thus decreasing the absorption cross-section of Photosystem II. Under these circumstances only a small degree of unstacking was detected by light scattering and measurements of the percentage of thylakoid length which is stacked to form grana. However, when considered on a surface area basis, the structural changes observed can qualitatively account for the magnitude of the chlorophyll fluorescence quenching due to the lateral diffusion of LHC.

Introduction

The phosphorylation/dephosphorylation of the light-harvesting chlorophyll *a*/*b*-protein complex (LHC) seems to be the underlying process for regulating light distribution between Photosystem I (PS I) and Photosystem II (PS II) in green plants and algae [1–4]. Phosphorylation of the LHC surface occurs when PS II is over-excited relative to PS I so that the intersystem plastoquinone (PQ) pool becomes reduced and a membrane-bound protein kinase is activated [5,6]. When the pool of PQ is oxidized, for example under conditions when PS I is over-excited relative to PS II, the protein kinase is inactivated and net dephosphorylation is brought about by a membrane-bound phosphatase [7].

Control of distribution of excitation energy between the two photosystems by reversible phos-

Abbreviations: DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; F_m, maximum chlorophyll fluorescence; LHC, light-harvesting chlorophyll *a*/*b*-protein complex; PQ, plastoquinone; PS, photosystem; Tricine, *N*-(2-hydroxy-1,1-bis(hydroxymethyl)ethyl)glycine.

phorylation of LHC has been detected by changes in chlorophyll fluorescence yield [5,6,8,9] and also by changes in the quantum efficiency of the two photoreactions [10,11]. Several mechanisms have been proposed explaining how a protein phosphorylation-induced alteration in the organisation of pigment-protein complexes may bring about this redistribution of excitation energy. These mechanisms involve changes in spillover [2,12], relative antenna size of the two photosystems [13–15] and radiationless decay [16].

With isolated thylakoids the precise affect of phosphorylation of LHC is highly dependent on the Mg^{2+} concentration of the suspending medium. When the Mg^{2+} level is high (5–10 mM) LHC phosphorylation appears to bring about a change in the absorption cross-section of the two photosystems in favour of PS I [13,15]. However, at lower levels of Mg^{2+}, the redistribution of incoming quanta in favour of PS I, due to LHC-phosphorylation, seems to involve changes in energy transfer between the two photosystems (spillover) as well as alterations in absorption cross-section [13,15].

The interplay between phosphorylation of LHC and the background Mg^{2+} level is to be expected if the mechanism of energy redistribution is based on phosphorylation-induced changes in the electrical charge characteristics of the thylakoid membrane surface [2,12,17]. It has been argued that phosphorylation introduces additional negative charges onto the exposed surfaces of LHC embedded in appressed granal lamellae and that this causes electrostatic repulsion between complexes and between adjacent membranes. As a consequence of this, a partial membrane unstacking may occur together with lateral movement of pigment-protein complexes into the non-appressed membranes which contain PS I [12]. Such a model is based on similar reorganisations which occur when coulombic repulsion is increased by lowering the cation levels of the suspending medium, thus reducing electrostatic screening of the surface charges [12,17]. These considerations suggest that at intermediate levels of screening cations, phosphorylation of LHC will have a strong affect on membrane organisation and that as the background cation level is raised the effect of LHC phosphorylation would be reduced or eliminated. In a study where the level of negative charge on the thylakoid surface was increased by the incorporation of linolenic acid it was found that a higher level of Mg^{2+} was required to maintain a membrane organisation normally observed with lower Mg^{2+} levels as judged by chlorophyll fluorescence measurements [18]. Such a finding is in line with the electrostatic control of thylakoid organisation detailed in articles by Barber [12,17,19]. However, although increasing the Mg^{2+} level does attenuate the effect of LHC phosphorylation on chlorophyll fluorescence, it does not totally inhibit the ATP-induced redistribution of energy [13,15,20].

In this paper we explore the relationship between LHC-phosphorylation-induced conformational changes and the effect of background cation levels in order to describe in more detail how changes in surface electrical charge may play a role in controlling excitation energy distribution to PS I and PS II.

Materials and Methods

Thylakoid suspensions were prepared by subjecting intact chloroplasts, isolated from peas by the method of Nakatani and Barber [21], to an osmotic shock in the reaction cuvette as described previously [15]. The basic reaction medium was as follows: 0.33 M sorbitol/10 mM Tricine/10 mM NaF/10 mM KOH, adjusted to pH 8.2 with HCl.

Protein phosphorylation of thylakoid membranes was brought about in the dark in two ways: either at different Mg^{2+} concentrations using NADPH and *Spirulina maxima* ferrodoxin to reduce the plastoquinone pool, as described previously, except that the chlorophyll concentration was 30 μg/ml and 20 μM DCMU was present (incubation time 50 min) [15]; or in a stock suspension at 100 μg/ml chlorophyll, contained in a sealed reaction vial with a fixed Mg^{2+} concentration (5 mM) using dithionite as reductant (incubation time 30 min) and 0.15 mM ATP. In the latter case the phosphorylated (plus ATP) and non-phosphorylated (minus ATP) thylakoids were diluted, washed and resuspended in the basic, unstacking, medium (20 mM monovalent cation with no divalent cation) containing 10 mM NaF to prevent dephosphorylation [15]. The phosphory-

lated and non-phosphorylated thylakoids were then stored on ice until use.

Chlorophyll fluorescence was excited by broad-band blue-green light (Schott glass filters, 2 mm BG18, 2 mm BG38 and Calflex C heat filter) and measured at 695 nm (the photomultiplier was protected by a Schott glass filter, RG695, 2 mm, and a 685 nm Balzer interference filter) as described previously [15]. Light scattering (90°) changes were measured at 549 nm (the photomultiplier was protected by a Schott glass filter, BG38, and a 549 nm Balzer interference filter). All reactions were carried out at room temperature.

Samples of phosphorylated and non-phosphorylated thylakoids for thin-section transmission electron microscopy were prepared as follows. Phosphorylation of thylakoid membranes was brought about by a modification of the dithionite method, described above, at a number of different Mg^{2+} concentrations in a 1.5 ml reaction volume. The reactions were terminated and fixation was brought about by addition of an equal volume of basic medium plus 0.83% glutaraldehyde, adjusted for the change in osmotic strength induced by the glutaraldehyde. The samples were then incubated for 5 min at room temperature, followed by 30 min on ice before preparation for thin-section electron microscopy essentially as described previously [22].

Results

The evidence that the control of excitation energy distribution by LHC phosphorylation involves an electrostatic mechanism is based on the differential response in the chlorophyll fluorescence yield of phosphorylated and non-phosphorylated thylakoid membranes to varying Mg^{2+} concentrations [15,20]. If an electrostatic process is operative then it should be possible to replace Mg^{2+} by other cations and detect a dependency on valency [19]. Fig. 1a and b shows how the fluorescence yield of phosphorylated and non-phosphorylated thylakoids varies as a function of the trivalent (Tris(ethylenediamine) cobaltic^{3+}) and monovalent (K^+ and Na^+) cation concentration of the suspension medium. For these experiments membranes were phosphorylated or non-phosphorylated at 5 mM $MgCl_2$ and then

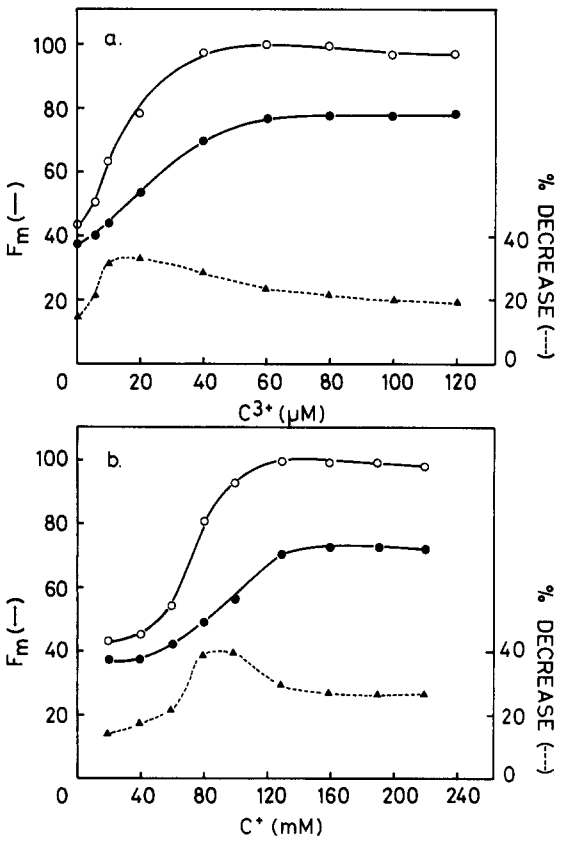


Fig. 1. The effect of protein phosphorylation on the chlorophyll fluorescence yield of pea thylakoids as a function of cation concentration: (a) trivalent; tris(ethylenediamine) cobaltic cation; (b) monovalent; K^+ plus Na^+. Thylakoids were phosphorylated (closed circles) or non-phosphorylated (open circles) by the dithionite method for 30 min and were suspended at 8 μg chlorophyll/ml in basic medium plus 20 μM DCMU and 10 mM NaF. Tris(ethylenediamine) cobaltic trichloride and KCl were added to give the total concentrations of tri- and monovalent cations as indicated and the suspensions were incubated at room temperature in the dark for approx. 20 min before measurement of the maximum level of chlorophyll fluorescence (F_m). Closed triangles show the percentage decrease in F_m due to phosphorylation.

washed free of residual divalent cations using a medium containing low levels of monovalent cations, a procedure which brings about thylakoid unstacking and a lowering of the maximum yield of chlorophyl fluorescence (F_m).

In both cases the phosphorylated membranes showed a higher concentration requirement for the cation-dependent increase in fluorescence yield when compared to non-phosphorylated mem-

branes, as indicated by the concentrations giving a half-maximal fluorescence increase ($C_{1/2}$ values). For the trivalent cation, $C_{1/2}$ values were increased by phosphorylation from 13 μM to 24 μM and for the monovalent cation from 74 mM to 92 mM. The effect of phosphorylation on the $C_{1/2}$ value was also found for the divalent cation, Mg^{2+}, but in this case the values were intermediate between those for trivalent and monovalent cations. The shift in $C_{1/2}$ due to phosphorylation for each cation and the sensitivity to valency ($C^{3+} > C^{2+} > C^{+}$) are characteristic of the electrostatic nature of the phenomenon.

The results in Fig. 1 also show an important feature in that, although intermediate levels of cations do partially overcome the phosphorylation-induced fluorescence lowering, at higher concentrations there is a cation-independent component (see percentage decrease traces in Fig. 1). This effect has previously only been reported for Mg^{2+} [15,20].

In order to investigate the effect of LHC phosphorylation on membrane conformation we have measured light scattering simultaneously with chlorophyll fluorescence as a function of the background level of screening cations. Phosphorylation was induced over a range of Mg^{2+} concentrations (0.5–7 mM), which would be expected only to affect membrane conformation and not the operation of the Mg^{2+}-dependent kinase, which is fully active at concentrations as low as 0.5 mM Mg^{2+} [20]. Fig. 2a and b shows the fluorescence and light scattering changes (expressed as a percentage of the maximum change observed with non-phosphorylated membranes) for non-phosphorylated and phosphorylated thylakoids. The fluoresence curves are essentially the same as those seen for tri- and monovalent cations (Fig. 1) and as reported by Horton and Black [20], with the ATP-induced fluorescence decrease being at its maximum at intermediate Mg^{2+} levels. However, in the case of light scattering (Fig. 2b) the difference between non-phosphorylated and phosphorylated membranes at high Mg^{2+} levels was less obvious, though a clear difference was seen at intermediate cation levels. After adjusting the fluorescence data of phosphorylated membranes to remove the cation-resistant component (see Fig. 2a), it can be seen that the remaining fluorescence decrease due to phosphorylation follows a curve similar to that obtained for the light scattering of non-phosphorylated membranes. This feature is emphasised in Fig. 2c, where the fluorescence changes have been plotted against the changes in light scattering. Non-phosphorylated and phosphorylated thylakoids show the same relationship between fluorescence and light scattering changes, provided that the adjusted fluorescence data is used for the phosphorylated membranes.

Because phosphorylation-induced light scattering changes were only clearly observed at the intermediate Mg^{2+} concentrations, we have in-

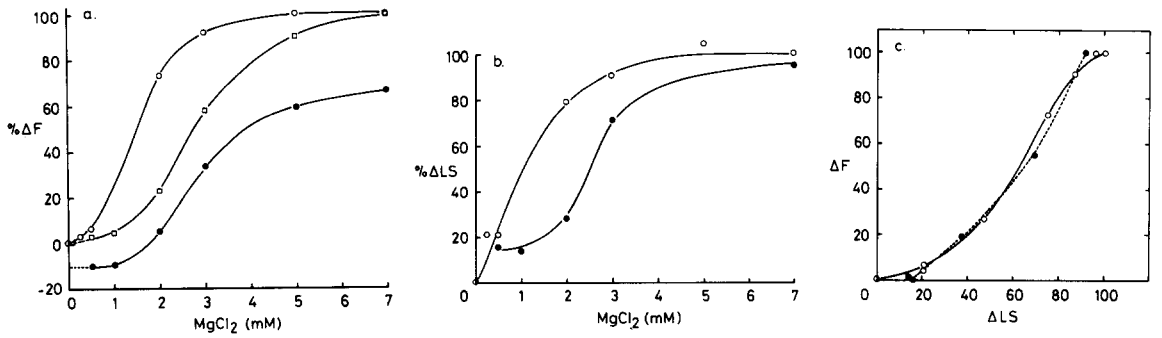


Fig. 2. (a) Chlorophyll fluorescence (ΔF) and (b) 90° light scattering (ΔLS) measured in isolated pea thylakoids phosphorylated (closed circles) or non-phosphorylated (open circles) at various Mg^{2+} concentrations using the NADPH and ferredoxin method. Fluorescence and light scattering levels, observed at the various Mg^{2+} concentrations, are expressed as percentages of the differences in fluorescence and light scattering seen between non-phosphorylated thylakoids in the absence of Mg^{2+} and either non-phosphorylated thylakoids (circles) or phosphorylated thylakoids suspended in 7 mM Mg^{2+} (squares). (c) The relationship between the percentage changes in fluorescence and light scattering as they vary with Mg^{2+} concentration for non-phosphorylated thylakoids (open circles) and phosphorylated thylakoids using the data normalised to a 100% change between 0 and 7 mM Mg^{2+} (closed circles).

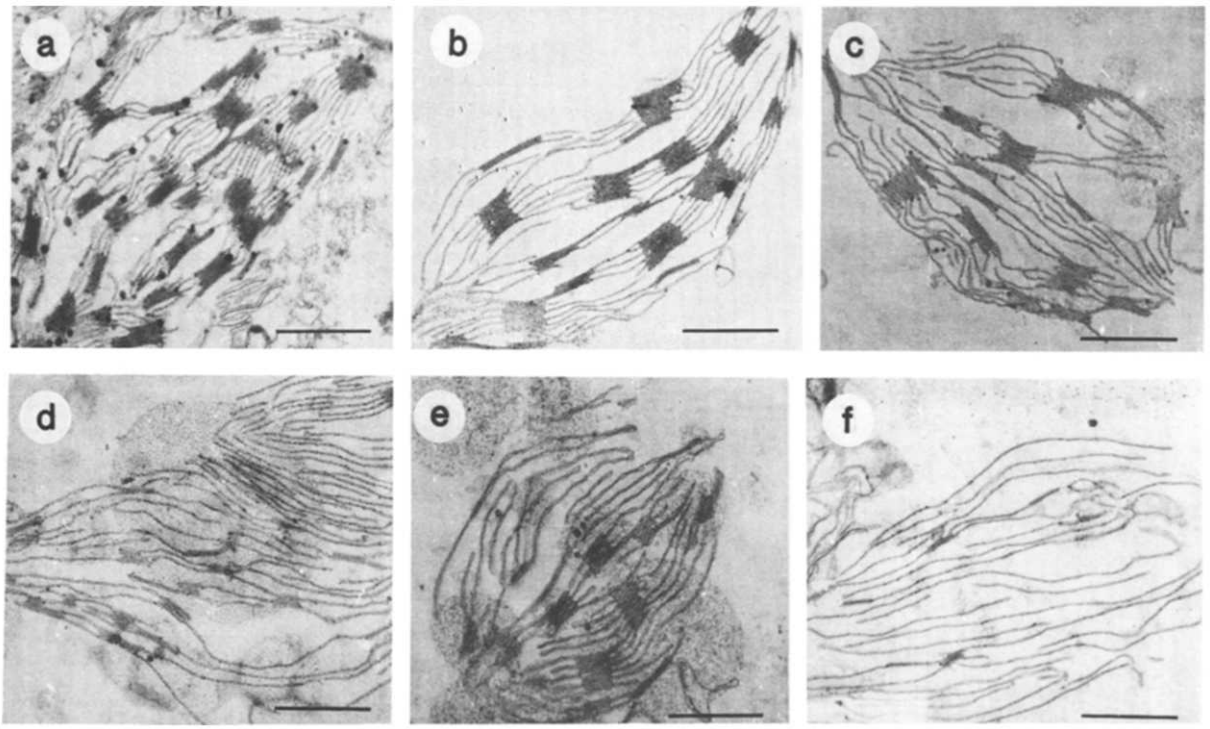
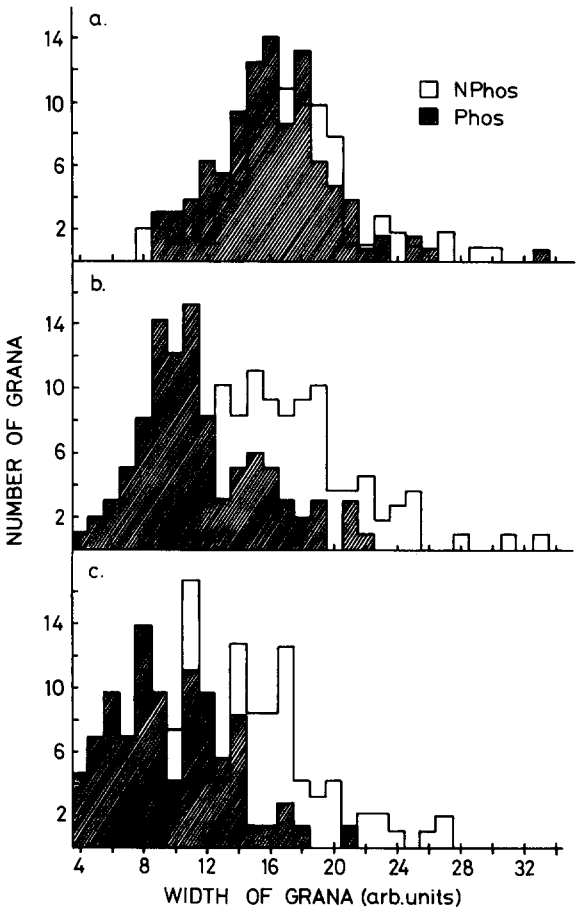


Fig. 3. Electron micrographs of pea thylakoids suspended at various Mg^{2+} concentrations and either phosphorylated (b,d,f) or not phosphorylated (a,c,e) using the NADPH and ferredoxin method. $MgCl_2$ concentrations were as follows: a,b, 5 mM; c,d, 2 mM; e,f, 1 mM. The bar is 1 μm.

vestigated the effect of phosphorylation on chloroplast structure directly from thin-section electron microscopy as a function of Mg^{2+} concentration. Fig. 3 shows examples of micrographs of thylakoids phosphorylated at 5, 2 and 1 mM $MgCl_2$ and their controls. It can be seen that in 1 and 2 mM Mg^{2+} the non-phosphorylated thylakoids are substantially stacked, while phosphorylated membranes show extensive unstacking when suspended in media containing these intermediate levels of Mg^{2+}. In 5 mM Mg^{2+}, however, phosphorylated membranes do not show any obvious change in the extent of stacking as compared to the non-phosphorylated membranes.

In order to quantify the effect of phosphorylation on stacking we have measured a number of parameters from electron micrographs: the frequency of grana of different widths, the number of grana per chloroplast and the percentage of thylakoids which are stacked compared to the total length of thylakoids. Fig. 4 shows histograms of the frequency of grana at different widths. It emphasises the structural difference between non-phosphorylated and phosphorylated thylakoids at the lower Mg^{2+} concentrations and also suggests that there may be a small amount of unstacking due to phosphorylation at 5 mM Mg^{2+}.

Table I shows the parameters measured from the electron micrographs including those obtained with non-phosphorylated thylakoids suspended in 0.5 and 0 mM Mg^{2+}. It also shows fluorescence and light scattering data that were obtained with the same thylakoid preparations after incubation under identical conditions to those which were used for electron microscopy. It can be seen that not only does the average granal width decrease of phosphorylation at intermediate Mg^{2+} concentrations, but so does the number of grana per chloroplast. Table I also shows that the length of stacked thylakoids as compared to the total length of thylakoids (expressed as a percentage) is substantially decreased at the lower Mg^{2+} concentrations.



In fact, at 1 mM Mg^{2+} the phosphorylated membranes are essentially unstacked. In this experiment the changes in fluorescence and light scattering were seen to be comparable with the data of Fig. 2a and b.

It is of interest that there is a 10% decrease in thylakoid stacking induced by phosphorylation at 5 mM $MgCl_2$ (Fig. 4, Table I). This is shown more clearly in Fig. 5, where the relative amount of stacking at different Mg^{2+} concentrations for both non-phosphorylated and phosphorylated membranes (assuming that the non-phosphorylated, 5 mM Mg^{2+} represents the maximum possible stacking) is plotted against Mg^{2+} concentration. Fig. 5 also shows the close correlation between light scattering changes and percentage stacking as measured from the length of appressed thylakoids.

Fig. 4. Histograms of the frequency of grana of different widths as a function of Mg^{2+} concentration and LHC phosphorylation. The values were obtained from the series of electron micrographs of the pea thylakoid samples in Fig. 3. The average width of a proportion of grana was measured in 12–16 chloroplasts. $MgCl_2$ concentrations were as follows: a, 5 mM; b, 2 mM; c, 1 mM. Nphos, non-phosphorylated; Phos, phosphorylated.

TABLE I

THE EFFECT OF Mg^{2+} CONCENTRATION AND LHC PHOSPHORYLATION ON MEMBRANE STACKING, CHLOROPHYLL FLUORESCENCE AND 90° LIGHT SCATTERING

Granal width and grana/chloroplast were measured in 12–16 chloroplasts. Percentage thylakoids stacked is length of granal thylakoids/total length of thylakoids × 100, measured in 5–8 chloroplasts. Percentage changes in fluorescence (F) and light scattering (LS) were measured after dilution to 40 μg chlorophyll/ml with basic medium plus 20 μM DCMU and the Mg^{2+} concentrations indicated. Percentage changes were calculated as described for Fig. 2.

Experimental conditions		Granal width (nm)	Grana/chloroplast	Thylakoids stacked (%)	$\%\Delta F$	$\%\Delta LS$
mM Mg^{2+}	Phos					
5	−	480 ± 120	24.5	66	100	100
5	+	430 ± 99	23.5	58	64	90
2	−	451 ± 95	23.0	63	89	96
2	+	332 ± 101	14.8	26	24	46
1	−	403 ± 114	21.0	49	47	52
1	+	281 ± 97	12.8	10	5	4
0.5	−	312 ± 126	16.7	18	18	29
0	−	261 ± 120	8.3	4	0	0

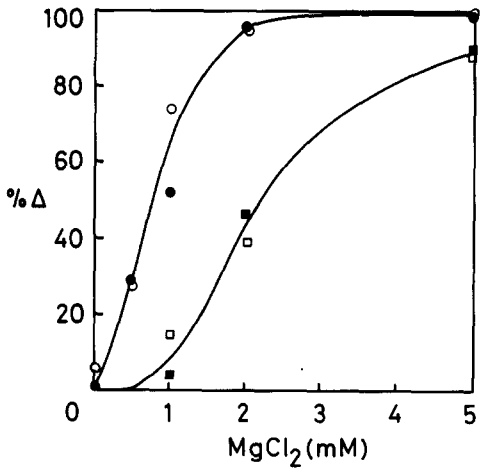


Fig. 5. Comparison of the percentage changes in stacking, measured from electron micrographs (open symbols), and from the 90° light scattering data of Table I (closed symbols), as a function of Mg^{2+} concentration, with (squares) and without (circles) LHC phosphorylation. Percentage change in stacking was calculated from the data of Table I assuming that non-phosphorylated thylakoids at 7 mM $MgCl_2$ have maximum stacking.

Discussion

The results presented in this paper are consistent with the general concept that the phosphorylation of LHC induces a reorganisation of thylakoid structure via alterations in the electrical properties of the membrane surface. It seems that the introduction of additional negative charges by the phosphorylation process is sufficient to alter the balance between the coulombic repulsive and van der Waal's attractive forces which exist between the exposed portions of the intrinsic proteins and between adjacent membrane surfaces [23]. This is clearly supported by the ability of cations of different valency to induce the chlorophyll fluorescence increase, and presumably membrane stacking, after phosphorylation of LHC.

As noted previously [15,20], over a concentration range of Mg^{2+} from 0.5 to 5 mM, the relative degree of fluorescence decrease induced by phosphorylation was not constant. At intermediate levels of Mg^{2+} the ATP-induced fluorescence decrease seems to involve both intersystem energy transfer and absorption cross-section changes, whereas at higher Mg^{2+} levels the fluorescence decrease due to LHC phosphorylation is less and seems to be due only to changes in absorption cross-section [15,20]. This latter component of the the fluorescence decrease is not overcome by adding excess Mg^{2+}, K^+ or trivalent cation, which is consistent with the idea that phosphorylated LHC carries sufficient additional negative charge to prevent is from repartitioning into the appressed membranes of the grana and therefore remains more intimate with PS I complexes in the non-appressed stromal lamellae [2,4,14,24].

At intermediate Mg^{2+} levels it is clear from light scattering and thin-section electron microscopy that the ATP-induced fluoresence decrease correlates with thylakoid unstacking. Such a result is to be expected when the electrostatic screening is sub-optimal and reinforces the concept that membrane phosphorylation brings about a perturbation of the forces which control thylakoid stacking and spatial interactions between PS II and PS I. The increase in the $C_{1/2}$ required for the cation-induced fluoresence increase relative to that required by non-phosphorylated membranes is to be expected if there is an increase in the net surface charge density due to protein phosphorylation. The results in Fig. 2 and of Horton and Black [20] emphasise that whereas in non-phosphorylated membranes the fluorescence increase is saturated at approximately 3 mM Mg^{2+}, phosphorylated membranes require more than 5 mM Mg^{2+}. Because of the electrostatic nature of this effect the actual concentration requirement for the cation-induced fluorescence increase may vary as it will depend on the background monovalent cation concentration [19]. For this reason care is needed in specifying precise values for Mg^{2+} concentration effects, which can cause inconsistencies when comparing data from different laboratories.

At the higher levels of Mg^{2+} the relationship between the fluorescence decrease and stacking looks, at first sight, to be less clear. However, a small change in the degree of stacking, measured as changes in the width of grana, can be significant in terms of displacement of LHC from the appressed to the non-appressed lamellae. According to our data (Table I) the difference in granal width at 5 mM Mg^{2+}, before and after phosphorylation, was about 50 nm where the initial width was 480 nm. Accepting that the granal membranes are circular and that there was no

decrease in the number of grana per chloroplast, then such a change represents a 20% decrease in the appressed area. Looked at in this way it is concluded that the reduction in appressed membrane area is qualitatively consistent with the magnitude of the ATP-induced chlorophyll fluorescence decrease measured at this Mg^{2+} concentration.

There have been various reports on the effect of LHC phosphorylation on membrane conformation measured by a number of techniques [4,14,25–27]. The extent of unstacking does seem to be species-dependent (e.g., greater in phosphorylated thylakoids from pea as compared to barley) but the variations within one species may be due to using 5 mM Mg^{2+}, which is within the range which may not fully screen the charges on the phosphorylated membranes (see Fig. 2).

So far only indirect data (changes in chlorophyll fluorescence and membrane conformation) indicate that the effect of LHC phosphorylation on excitation energy distribution between the photosystems is due to an increase in surface charge density. The more direct 9-aminoacridine technique has not shown a difference [28,29]. However, it was suggested that the expected change would be too small to be demonstrated by this technique [28]. Preliminary electrophoretic mobility studies using laser Doppler cytopherometry have also not shown a large change in electrophoretic mobility between phosphorylated and non-phosphorylated membranes (Telfer and Barber, unpublished data). Comparison with work on thylakoid membranes treated with linolenic acid [18] suggests that the chlorophyll fluorescence yield changes induced by phosphorylation would only result in a very small change in mobility which might be difficult to demonstrate by laser Doppler cytopherometry.

In conclusion, the above results and discussion support the idea that above 5 mM Mg^{2+} the phosphorylation of LHC within the appressed granal area is sufficient to disturb its surface charge characteristics and induce a partial unstacking. The phosphorylated LHC is then free to intermix with the PS I complexes, located in non-appressed membranes, where it acts as the antenna system for PS I. As the Mg^{2+} concentration is lowered the additional charges due to surface phosphorylation have a more dramatic effect on organisation due to poor electrostatic screening. Under these circumstances there is extensive unstacking and a randomisation of PS II, PS I and LHC which brings about changes in energy transfer from PS II to PS I as well as altering the absorption cross-sections of the two photosystems. So far no freeze-fracture studies have been carried out on phosphorylated membranes at these lower Mg^{2+} concentrations, but under these circumstances we predict that particle size distribution on the four fracture faces, commonly seen, would support these conclusions.

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