ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 57, nr 3: 401-418
1988

Acyl lipids in the supramolecular chlorophyll-protein complexes of photosystems – isolation artifacts or integral components regulating their structure and functions?

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(Received: March 15,1988. Accepted: March 31,1988)

Abstract

The precise nature of interactions between the chloropnyll-protein complexes related to photosystem I or photosystem II and the acyl lipids in the thylakoid membranes is not yet fully elucidated. Analyses of the lipid content of isolated photosystem supramolecular complexes reveal that they are integral components of these complexes. However, the relations between certain acyl lipids and the specific structure and functions of the complexes investigated are still widely discussed. The most generally accepted phenomenon is the fact of participation of phosphatidylglycerol containing the unique *trans*-Δ^3--hexadecenoic acid in the oligomerization of the light-harvesting chlorophyll a/b protein complex II.

Key words: acyl lipids, chlorophyll-protein complexes, photosystems, thylakoid membranes

INTRODUCTION

Photosynthesis in green plants is carried out by a highly organized system of the thylakoid membranes. These membranes may be described in terms of a mosaic model with integral globular proteins being dispersed in a fluid lipid matrix. The proteins constitute about 60% of the membrane material while the acyl lipids and pigments account for the remaining 40%. The majority of the membrane proteins consist of four types of chlorophyll-protein complexes, i.e. the photochemically active chlorophyll a-proteins containing photocenters I or II surrounded by antennae chlorophyll and photochemically inactive

light-harvesting chlorophyll a/b protein complexes I and II. It is now clearly established that all chlorophyll and carotenoids in the thylakoids of higher plants are non-covalently bound to proteins associated in the supramolecular complexes mentioned above.

The refinement of solubilization and analysis techniques has allowed for the extraction of these supramolecular complexes closer to the "*in vivo*" state. Progress in the analysis of chl-protein complexes in the last decade has resulted in accumulation of evidence indicating the presence of acyl lipids as an integral constituent of these complexes and suggesting their indispensability for proper structural organization and function. Much evidence concerning some aspects of the involvement of acyl lipids in the structure and function of thylakoid membranes has recently been summarized by Rawyler and Siegenthaler (1986) and the reader is kindly advised to consult that volume.

PHOTOSYSTEM I

About 85% of PSI complexes are located in unstacked regions of grana (stroma thylakoids). The PSI particles contain the so-called "core complex I" which is functionally competent and to which specific light-harvesting a/b protein antenna complexes I (LHCIa and LHCIb) are bound. A number of methods for isolation and purification of the PSI complex have been published. Depending on the principle of the method they can be divided into two groups. The methods utilizing non-denaturating polyacrylamide gel electrophoresis of the thylakoid membranes gently solubilized with detergents (sodium or lithium dodecyl sulfate, sodium deoxycholate, octyl glucoside, Triton X-100) result in the resolution of different chl-protein complexes, among them CP1a (oligomer) and CP1 (monomer) which are related to the reaction centre of PSI (Hayden and Hopkins 1977, Waldron and Anderson 1979, Camm and Green 1980, Henry and Siegenthaler 1981, Picaud et al. 1982, Noben et al. 1983, Vierling and Alberte 1983, Huner et al. 1987a). The methods of the second group are based upon solubilization of the thylakoid membranes with Triton X-100, separation of the extract during sucrose gradient centrifugation in the presence of low concentrations of Triton X-100, resulting in purified PSI particles retaining their LHC's. These particles usually exhibit a chlorophyll to P700 ratio of 110-200 and contain 11-13 polypeptides related to the reaction centre and antenna complexes. The widely accepted model of this method (Mullet et al. 1980a, b) is sometimes modified by adding some extra procedures allowing better characterization of the properties of these particles and their constituents (Bassi and Simpson 1987). It should be underlined that PSI particles obtained by these procedures have the same properties as a high-molecular mass complex CP1a resolved by non-denaturing gel electrophoresis. Detailed descriptions of the structure and function of PSI complexes have been published recently (Staehelin 1986, Thornber 1986, and refs. therein).

Although the acyl lipid composition of the thylakoid membranes is very well known, the question whether these lipids are the integral constituents of chl-protein complexes and not artifacts created by the isolation and purification of the complexes from thylakoid membranes and whether they play a role in the structure and functions of these complexes, still remains open. Thus, considerations concerning this problem should start from the qualitative and quantitative composition of acyl lipids in the thylakoid membranes. Table 1 shows the average acyl lipid content in the thylakoid membranes isolated

Table 1

The average acyl lipid content in the thylakoid membranes isolated from different plants

Acyl lipid	Average value (mean ± SD)
MGDG	47.1 ± 4.7
DGDG	30.2 ± 4.6
SQDG	8.0 ± 2.8
PG	10.9 ± 2.7
PC	3.8 ± 1.1

The results for calculations were taken from:
Chapman et al. 1984 (*Amaranthus retroflexus, Poa annua, Senecio vulgaris*),
Gounaris et al. 1983, 1984a (spinach),
Guillot-Salomon et al. 1982 (pea, barley),
Henry et al. 1984 (barley),
Huner et al. 1987a (rye),
Krupa 1982 (bean),
Krupa 1988 (radish cotyledons),
Krupa and Baszyński 1985 (tomato),
Murphy and Woodrow 1984 (spinach),
Rawyler and Siegenthaler 1981a (spinach),
Tuquet et al. 1984 (spinach).

from different plants. This will be the starting point to determine to what extent the content of acyl lipids is unique for PSI or other complexes discussed in this article. Unfortunately, it has not yet become a common practise to analyse the lipid composition of chl-protein complexes isolated by different methods and from different sources. Table 2 summarizes such results obtained for PSI complexes during the last decade. It should be underlined that although sometimes a relative percentage of each acyl lipid in the total content is similar to that in whole thylakoids, their amounts are usually more than several times lower because of the isolation procedures removing, as is supposed, all lipids forming the bilayer structure of the membrane. Thus, the acyl lipids reported here may be considered as integral constituents of these complexes. The method used and the kind of detergent employed are largely responsible for some differences in the lipid compositions showed in Table 2.

Table 2

A comparison of the acyl lipid composition of PSI supramolecular complexes isolated by various methods

Acyl lipid	% Of total content									
MGDG	–	45.0	57.2	12.5	46.2	56.1	50.4	41.0	34.8	34.0
DGDG	–	27.0	21.4	21.9	27.1	23.7	25.9	28.6	13.0	25.2
SQDG	72.8	23.0*	–	34.4*	7.0	5.7	5.9	23.1	39.1	13.4
PG	–	5.0	14.3	31.3	13.1	9.4	10.5	5.3	8.7	13.3
PC	–	–	7.1	–	6.6	5.2	7.3	2.0	4.3	14.0
PI	27.8	–	–	–	–	–	–	–	–	–
Source	spinach (1)	tobacco (2)	tobacco (3)	pea (4)	pea (4)	pea (4)	barley (4)	barley (4)	tobacco (5)	spinach (6)

* SQDG + PC
(1) – Rawyler et al. 1980
(2, 3) – Tremolieres et al. 1981, 1982,
(4) – Guillot – Salomon et al. 1982,
(5) – Remy et al. 1982,
(6) – Tuquet et al. 1984.

As can be easily calculated, the chl-protein complexes of the reaction centers of PSI or PSI particles are on the whole relatively enriched with sulfolipid (SQDG) and to some extent with phosphatidylglycerol (PG). The relative proportions of monogalactolipid (MGDG) and digalactolipid (DGDG) are lower than those in whole thylakoid membranes. The participation of SQDG in the structure and function of PSI was postulated by Krupa and Baszyński (1977) in their extraction-reconstitution studies on thylakoid membranes and by Menke and his group (Radunz and Berzborn 1970, Menke et al. 1976, Schmid et al. 1978, Radunz et al. 1984a) on the basis of immunological studies on the localization and function of sulfolipid in thylakoids. This could be achieved by the conformational changes caused by SQDG in certain PSI polypeptides. The presence of SQDG as the major lipid class in PSI particles was shown by Rawyler et al. (1980) although the accompanying high amounts of phosphatidylinositol (PI) in these particles are somewhat confusing because this lipid is detected in very low amounts in thylakoid membranes and it is not even widely recognized as an integral component of these membranes. The role of certain membrane acyl lipids in the structure and function of PSI has been postulated by Krupa (1983, 1984a, b) on the basis of the effect of some lipolytic enzymes (phospholipases A_2, C, D, galactolipase) on the polypeptide patterns and chl-protein complexes of enzyme-treated thylakoids. These studies resulted in the proposed array of indispensable acyl lipids for the integrity and stability of chl-protein complexes of photosystem I:

$$CP1a + CP1 - MGDG > DGDG > PG > PC.$$

These results confirmed, in fact, the earlier studies carried out in our laboratory, pointing out the role of galactolipids in PSI activity in

heptane-extracted thylakoids (Krupa and Baszyński 1975). During aging *in vitro* of purified thylakoid membranes a considerable decrease in DGDG content (and also in that of PG and SQDG) was followed by the decomposition of CP1a – the oligomeric form of CP1 (Henry et al. 1982). In a series of elegant and well documented papers originating from Siegenthaler's group it was clearly shown that MGDG and PG are mainly distributed in the outer leaflet of the thylakoid membrane, being thus closely associated with PSI particles (Rawyler and Siegenthaler 1980, 1984, 1985, Siegenthaler 1982, Giroud and Siegenthaler 1984, Siegenthaler and Giroud 1986, Rawyler et al. 1987). A certain specific pool of PG molecules may also be involved in the non-cyclic electron flow from H_2O to $NADP^+$ (Rawyler and Siegenthaler 1981a, b, Siegenthaler et al. 1987). From these papers, albeit indirectly, one can assume the importance of certain acyl lipid domains for the functioning of PSI particles. A conclusion about the molecular interactions between the photosynthetically active proteins of photosystem I and MGDG and PG has already been drawn from the serological studies on the function of galacto- and phospholipids in the thylakoid membrane (Radunz 1984, Radunz et al. 1984b).

The opinion that galactolipids might not be fixed to a certain chl-protein complex and specific associations between endogenous galactolipids and chl-protein complexes are not evident (Heinz and Siefermann-Harms 1981) seems to be rather irrelevant. However, it must be honestly emphasized that all the evidence concerning the role of certain acyl lipids in the structure and function of PSI complex has come rather from indirect studies. No reports have yet been published dealing with isolated and purified PSI particles and the effect of their acyl lipid composition or its changes on the structure--function relations.

PHOTOSYSTEM II

Photosystem II domains in thylakoid membranes are composed of the so-called "core-complex" containing the reaction center. The polypeptides of the water splitting system and light-harvesting chlorophyll a/b protein complex II (LHCII) being primarily the energetic antenna for PSII and containing about half of the total chlorophyll of photosystems, are attached to the "core complex". Because the PSII reaction centre can be easily separated from its light-harvesting system and characterized separately, this chapter will be divided into two parts discussing the role of acyl lipids in that reaction centre as well as in its LHCII.

CORE COMPLEX II

The PSII core complex can be isolated from thylakoid membranes by different modifications of non-denaturating gel electrophoresis (CPa complex), as was discussed in Chapter 2 of this review, or by specialized methods of extraction using different detergents (Triton X-100, digitonin, octyl glucoside),

followed by sucrose gradient centrifugation, Sepharose or DEAE cellulose columns, isoelectrofocusing (Satoh 1979a, Berthold et al. 1981, Lam et al. 1984, Gounaris and Barber 1985, Ikeuchi et al. 1985, Satoh et al. 1985, Ghanotakis and Yocum 1986). Usually such highly purified preparations contain 5 polypeptides of apparent molecular weights 47, 43, 33, 30 and 10 kD, chlorophyll a, some amounts of chlorophyll b, β-carotene, pheophytin, plastoquinone-9 and, depending on the method of isolation and purity of the preparations, some amounts of acyl lipids (e. g. Gounaris and Barber 1985).

The acyl lipid compositions of PSII particles, reaction centers or CPa complexes have very rarely been investigated. The results of these investigations summarized in Table 3 show that SQDG, besides MGDG, may be

Table 3

A comparison of the acyl lipid composition of PSII supramolecular complexes isolated by various methods

Acyl lipid	% Of total content					
MGDG	70.0	14.0	34.9	39.7	54.0	29.7
DGDG	10.0	5.0	6.7	29.1	23.0	–
SQDG	–	50.0	16.4	8.7	5.0	70.3
PG	–	10.0	27.2	15.7	7.0	–
PC	20.0	–	14.9	6.8	12.0	–
Source	tobacco (1)	tobacco (2)	spinach (3, 4)	spinach (5)	*Senecio vulgaris* (6)	spinach (7)

(1) – Tremolieres et al. 1982,
(2) – Remy et al. 1982,
(3. 4) – Gounaris et al. 1983, 1984a,
(5) – Tuquet et al. 1984,
(6) – Chapman et al. 1984,
(7) – Gounaris and Barber 1985.

recognized as the major acyl lipid component of the PSII reaction centre. The relative amount of PC is also considerably higher than that in whole thylakoid membranes, while that of DGDG is much lower. How can this data be interpreted? Unfortunately, the situation is very similar to the investigations on PSI particles reported earlier in this review. The lack of direct evidence of the participation of some acyl lipids in the structure and function of the PSII reaction centre allows us to draw only rough conclusions from the available data. Let us start our considerations from PC – the acyl lipid which is most frequently referred to PSII. In the opinion of Siegenthaler and his coworkers PC is the main lipid associated with the thylakoid structures responsible for PSII activity (Rawyler and Siegenthaler 1980, 1981b, Siegenthaler et al. 1987). Radunz (1980, 1981, 1984) in his serological investigations on the distribution and function of phospholipids found that in normally functioning thylakoid membranes PC can be a component of the active PSII. A number of

papers (Murphy 1984, Murphy and Knowles 1984, Murphy and Woodrow 1984) discussed an important functional role of PC as the lipid environment in PSII electron transport and energy transfer to PSI. The role of certain acyl lipids such as PC and DGDG in optimisation of the tertiary organisation of PSII proteins leading to maximal activity of this photosystem has been underlined by Gounaris et al. (1983, 1984a, b). The necessity of PC and some other acyl lipids for the integrity of the CPa complex related to the reaction centre of PSII has been extensively investigated by Krupa (1983, 1984a, b) using a number of lipolytic enzymes such as phospholipase A_2, C, D and galactolipase. The conclusions drawn from these studies showed that the importance of acyl lipids for the integrity and functional stability of CPa complex could be presented as follows:

$$\text{CPa} - \text{PC} > \text{MGDG} > \text{DGDG} > \text{PG}.$$

In 1985 Gounaris and Barber reported the isolation and purification of the lipoprotein complex being the photochemically active reaction centre complex of PSII. Only two acyl lipids were present in this complex – MGDG and SQDG, the former being relatively more abundant. Both lipid classes in the PSII reaction centre were of a very low degree of unsaturation as compared with their counterparts in the thylakoid membranes or PSII membrane preparations. The sufficiently low levels of acyl lipids co-purifying with the complex and a lipid composition very uncharacteristic for the bilayer distinctly indicate that the PSII reaction centre is a lipoprotein-pigment complex. Whether specific types of bonds exist between these lipids and the protein is not definitely known at present. According to Chapman et al. (1984) and Thomas et al. (1984) a significant part of the total thylakoid MGDG is *in vivo* concentrated in the lipid matrix around PSII and may be involved in the packaging of this photosynthetic reaction centre into the thylakoid membrane and its correct supramolecular organization. Some attention should be drawn to the role of SQDG in the PSII reaction centre. As can be seen from Table 3 its relative amounts in this supramolecular complex are considerably higher than in thylakoids (compare Table 1). SQDG was postulated earlier (Anderson 1975) to be, together with PG, the predominant specific externally located boundary lipid of chl-protein complex II. Unitt and Harwood (1982) suggested the localization of SQDG in the inner leaflet of the thylakoid membrane, thus closer to PSII. Radunz's recent experiments with antisera against SQDG have endorsed the indirect involvement of this lipid in PSII activity (Radunz et al. 1984a). It participates in the conformational changes of proteins involved in the electron transport reactions.

Recently, some attempts have also been made to connect the PG containing *trans*-Δ^3-hexadecenoic acid with the O_2 evolution in PSII using phospholipase A_2 (Tuquet et al. 1984) but the concomitant hydrolysis of the total PC pool in isolated PSII particles brings in question the final conclusion about the involvement of PG in the oxygen evolution activity. Moreover, Gounaris et al. (1983, 1984a, b) showed that PG and SQDG added to isolated PSII particles completely inhibited the O_2 evolving system.

LIGHT-HARVESTING COMPLEX II

Light-harvesting chlorophyll a/b protein complex II (LHCII) is not essential for photosynthetic competence but functions as a light harvesting assembly, primarily for photosystem II (Thornber 1986). The LHCII complex alone accounts for about half of the total membrane protein and chlorophyll content and therefore is of special importance from the standpoint of the thylakoid membrane structure. Apart from its function as an antenna that collects light energy, this complex regulates the transfer of excitation energy to the reaction centers of PSII and PSI, depending on the phosphorylation of its apoprotein (Bennet et al. 1984, Staehelin 1986). The complex also mediates the interaction of thylakoid membranes, which leads to the formation of stacks of membrane vesicles — the chloroplast grana (Staehelin 1986). A three-dimensional map of this complex shows that the LHCII is a highly asymmetric transmembrane protein composed of three structurally equivalent monomers. A large surface area exposed on one side of the oligomeric complex suggests a functional role in membrane interactions (Kühlbrandt et al. 1983, Kühlbrandt 1984, Li 1985). The ability of LHCII from widely different plant species to form such oligomeric supramolecular arrays suggests that this structure is of general significance.

Several different methods have been used to obtain pure LHCII preparations. In the primary steps of purification, all of them utilize detergents such as digitonin, SDS or Triton X-100. Final steps of purification were made with preparative polyacrylamide gel electrophoresis (Picaud et al. 1982), sucrose gradient centrifugation (Burke et al. 1978, Foyer and Hall 1979, Mullet and Arntzen 1980), column chromatography (Dunkley and Anderson 1979, Thornber and Thornber 1980, Süss 1983), isoelectrofocusing (Satoh 1979b, Larkum and Anderson 1982) or phase-partition systems (Albertsson and Andersson 1981). Recently, the simple and rapid "method of successive precipitations", the results of which was reproducible isolation of large quantities of highly purified LHCII from various plants, has been developed by Krupa et al. (1987a). Isolated LHCII preparations, irrespective of the procedure used, usually contain 2-4 polypeptides with apparent molecular weights in the range of 26-29 kD. A low chlorophyll a/b ratio of 1.0-1.2 is very characteristic for this complex.

As was mentioned in the previous chapters, analyses of the acyl lipid composition of isolated photosynthetic supramolecular complexes are, in fact, not very common. From the data summarized in Table 4 it can be clearly seen that the isolated LHCII preparations are specifically enriched with PG. Moreover, it is well known that this phospholipid contains a unique fatty acid, *trans*-Δ^3-hexadecenoic acid (*trans*-16:1) which is specifically bound to PG molecules in position *sn*-2 only (Dubacq and Tremolieres 1983). From many recent works it also appears that it is the compound which plays a role in association of the protein subunits of the LHCII oligomer (Tremolieres et al. 1982, 1984, Huner et al. 1987a, b, Król et al. 1987, Krupa et al. 1987a, Williams et al. 1987, Krupa 1988). The investigations concerning the role of PG containing *trans*- 16:1 acid in the

Table 4

A comparison of the acyl lipid composition of LHCII preparations isolated by various methods

Acyl lipid	% Of total content								
MGDG	34.1	52.8	33.3	51.0	58.4	48.8	51.9	28.3	34.4
DGDG	29.1	26.1	29.0	28.0	15.5	13.4	29.4	25.3	28.4
SQDG	12.8	14.6	9.5*	6.0	3.6*	13.4	2.3	6.1	5.6
PG	15.7	6.5	28.2	15.0	5.5	21.2	12.6	33.3	29.7
PC	6.5	–	–	–	–	3.1	3.9	7.1	1.9
PI	1.7	–	–	–	–	–	–	–	–
Source	spinach (1)	spinach (2)	tobacco (3)	maize (4)	tobacco (5)	tobacco (6)	spinach (7)	rye (8)	radish cotyledons (9)

* – SQDG + PC

(1) – Rawyler et al. 1980,
(2) – Ryrie et al. 1980,
(3, 5) – Tremolieres et al. 1981, 1982,
(4) – Selstam 1981,
(6) – Remy et al. 1982,
(7) – Tuquet et al. 1984,
(8) – Krupa et al. 1987a,
(9) – Krupa 1988.

supramolecular structure of LHCII can be divided into two groups. The first one deals with the *in vitro* factors modifying the lipid and fatty acid composition of LHCII using lipolytic enzymes (Tremolieres et al. 1982, Krupa 1984a, b, Huner et al. 1987b, Krupa et al. 1987a) or using artificial liposomes specifically enriched with *trans*-16:1 acid (Remy et al. 1982, 1984a, b, Tremolieres et al. 1984). The second group refers to the *in vivo* studies on the effect of environmental conditions (e.g. light, herbicides, low temperature stress, heavy metals) or specific mutations (lack of *trans*-16:1 acid) on the structure and function of this chl-protein complex (Lemoine et al. 1982, Leech and Walton 1983, McCourt et al. 1985, Huner et al. 1987a, b, Król et al. 1987, Krupa et al. 1987a, b, Krupa 1988, Maroc et al. 1987, Williams et al. 1987). The effect of some *in vivo* and *in vitro* factors (low temperature stress, heavy metal treatment, lipolytic enzymes) affecting the content of *trans*-16:1 acid in the PG pool of isolated LHCII and its relationship to the level of LHCII oligomeric form is shown in Table 5. The results reported in this chapter and summarized in Table 5 unequivocally

Table 5

The relations between *trans*-Δ^3-hexadecenoic acid and the LHCII oligomer content in different environmental *in vivo* and *in vitro* conditions

Conditions	*Trans*-16:1/16:0 ratio	Monomer/oligomer ratio
Low temperature stress[1]		
control (+20°C)	1.48	0.50
treated (+5°C)	0.32	0.80
Heavy metal stress[2]		
control	2.21	1.84
cadmium	0.38	4.71
Lipolytic enzymes[3]:		
control	1.60	0.40
phospholipase A_2	—*	1.65

* – the complete hydrolysis of PG,
[1] – rye (Huner et al. 1987b, Krupa et al. 1987a),
[2] – radish cotyledons (Krupa et al. 1987b, Krupa 1988)
[3] – isolated rye LHCII (Huner et al. 1987b, Krupa et al. 1987a),

indicate a positive correlation between the level of *trans*-16:1 acid and the oligomerization of LHCII. The correlation coefficients ($R_{x,y}$) calculated for the relation between *trans*-16:1 and oligomer content reached values from 0.9644 (Huner et al. 1987a) to 0.9828 (Krupa 1988). This supports the hypothesis about the role of this fatty acid in the supramolecular organization of LHCII even if some authors' opinions are not quite clear on that point. Moreover, the results quoted here revealed that regardless of the kind of environmental stress, its final effect on LHCII was related to the characteristic shift in the *trans*-16:1

acid content towards the saturated palmitic acid (16:0) with the concomitant decrease in the oligomer/monomer ratio (Table 5). The primary mechanism generating this shift still remains unknown, although the inhibition of palmitate desaturase might be considered.

From the very beginning of this chapter our attention has been focused on the role of PG and *trans*-16:1 acid in the structure and function of the LHCII complex. However, this complex also contains other acyl lipids of which MGDG may as well be of some importance for the functioning of LHCII. Though previously questioned as an integral component of LHCII (Heinz and Siefermann-Harms 1981), it now seems to play some role in the energy transfer from LHCII to the photosystems (Siefermann-Harms et al. 1982). The importance of MGDG and DGDG, besides PG, for the proper organization and function of LHCII has also been underlined repeatedly by Krupa (Krupa 1983, 1984a, b, Krupa et al. 1987a) on the basis of experiments with the use of some lipolytic enzymes e.g. galactolipase, acting on thylakoid membranes, chl-protein complexes and isolated and purified LHCII. Although MGDG and DGDG appear not to be intimately related to the stabilization of oligomeric LHCII, they may be involved in the stabilization of chlorophyll-protein interactions since hydrolysis of the galactolipid pool of LHCII resulted in a significant increase of free pigments disjoined from the complex (Krupa et al. 1987a). The hypothesis of Rosenberg (1967) that galactolipids, because of their high content of polyunsaturated fatty acids (especially linolenic acid), would ensure the proper arrangement of chlorophyll molecules within chl-protein complexes should be reminded at this point.

It must be emphasized that probably not only *trans*-16:1-containing PG is involved in the stabilization of the oligomeric form of LHCII. It was shown during experiments on the effect of lipolytic enzymes on the structure of isolated LHCII that even after total hydrolysis of almost all, except one, acyl lipids (MGDG, DGDG, PG, PC) present in this complex – a small but considerable amount of LHCII in oligomeric form still remains stable (Krupa et al. 1987a). The exception mentioned above was SQDG, the only lipid hydrolyzed to a very low degree by the enzymes used about 90% left in LHCII preparations). Thus, the possible involvement of this strongly anionic lipid as a factor assisting PG containing *trans*-16:1 acid in the stabilization of the LHCII oligomer requires more detailed studies.

CONCLUDING REMARKS

In light of the studies presented in this review and concerning more or less directly the role of acyl lipids in the structure and function of the supramolecular chl-protein complexes of photosystems, it would be premature to propose a definite picture of such relationships. The only role that seems to be well documented and proved is that of *trans*-16:1-containing PG in oligomerization of the LHCII complex, although it should be definitely determined whether this specific form of PG is involved in the formation of the

LHCII oligomer or its stabilization, or both. It is too early to connect unambiguously the presence of a specific lipid class with the expression of a specific function of chl-protein complexes related to the reaction centers of PSI and PSII. However, some serious indications exist and they must be extensively investigated in the nearest future. Despite all the questionable cases mentioned above, in this author's opinion it is beyond doubt that acyl lipids are integral components of photosystem supramolecular complexes, regulating their structure and function.

It should be emphasized here that there is still a number of people questioning such close coexistence and interrelations between lipids and protein complexes in the thylakoid membranes. To them I would like to dedicate an excerpt from Francis Clifford's "The naked runner": "According to the theory of aerodynamics, and as may be readily demonstrated by means of a wind tunnel, the bumble-bee is unable to fly. This is because the size, weight and shape of his body in relation to the total wing span makes flight impossible. But the bumble-bee, being ignorant of these scientific facts and possessing considerable determination, does fly — and makes a little honey, too".

Acknowledgments

I dedicate this review to the memory of my Father. This work was supported by the project CPBP 05.02.

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Lipidy acylowe w supramolekularnych kompleksach chlorofilowo-białkowych fotoukładów — izolacyjne artefakty czy integralne składniki regulujące strukturę i funkcję?

Streszczenie

Nie wyjaśniono dotychczas dokładnie natury oddziaływań między kompleksami chlorofilowo-białkowymi fotoukładów i lipidami acylowymi błon tylakoidowych. Analizy składu lipidowego tych kompleksów wskazują na to, że lipidy acylowe są ich integralnymi składnikami. Przedyskutowano wyniki najnowszych badań dotyczących relacji między określonymi składnikami lipidowymi kompleksów chlorofilowo-białkowych, a ich strukturą i funkcją. Szczegółowo omówiono rolę kwasu *trans*-Δ^3-heksadecenowego w oligomeryzacji kompleksu antenowego II fotoukładu (LHCII) — najlepiej dotychczas poznany przykład wzajemnych oddziaływań lipid-białko w błonach tylakoidowych.