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Review

Glycerolipids in photosynthesis: Composition, synthesis and trafficking☆

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A B S T R A C T

Glycerolipids constituting the matrix of photosynthetic membranes, from cyanobacteria to chloroplasts of eukaryotic cells, comprise monogalactosyldiacylglycerol, digalactosyldiacylglycerol, sulfoquinovosyldiacylglycerol and phosphatidylglycerol. This review covers our current knowledge on the structural and functional features of these lipids in various cellular models, from prokaryotes to eukaryotes. Their relative proportions in thylakoid membranes result from highly regulated and compartmentalized metabolic pathways, with a cooperation, in the case of eukaryotes, of non-plastidic compartments. This review also focuses on the role of each of these thylakoid glycerolipids in stabilizing protein complexes of the photosynthetic machinery, which might be one of the reasons for their fascinating conservation in the course of evolution. This article is part of a Special Issue entitled: Dynamic and ultrastructure of bioenergetic membranes and their components.

1. Introduction

The glycerolipid composition of photosynthetic membranes (thylakoid lipidome) has been remarkably conserved in the course of evolution, from cyanobacteria to chloroplast-containing eukaryotes [1–3]. Glycerolipids are a category of lipids having a 3-carbon glycerol scaffold (each carbon is numbered following the stereospecific numbering nomenclature *sn*-1, *sn*-2, *sn*-cp3), harboring one or two acyl chains esterified at positions *sn*-1 and *sn*-2, and a polar head at position *sn*-3 (Fig. 1). Table 1 shows that primary chloroplasts (i.e. photosynthetic plastids deriving from a primary endosymbiosis), analyzed from green algae to vascular plants [4–6], have a unique glycerolipid composition compared to other subcellular compartments: they are characterized by a very low content in phosphoglycerolipids, mostly PG (phosphatidylglycerol), PC (phosphatidylcholine), and PI (phosphatidylinositol), and a very high content in glycoglycerolipids that contain no phosphorus, mainly MGDG (monogalactosyldiacylglycerol), DGDG (digalactosyldiacylglycerol) and SQDG (sulfoquinovosyldiacylglycerol). This table also shows that MGlcDG (monoglucosyldiacylglycerol) is uniquely detected in cyanobacteria and is not found in chloroplasts. These very basic observations highlight the conservation of a quartet of lipids, i.e. MGDG, DGDG, SQDG and PG, from cyanobacteria to primary chloroplasts and raise questions regarding (*i*) the roles that these lipids may have in photosynthesis and (*ii*) the molecular processes establishing and regulating this unique lipid profile. Here, we summarize our current knowledge on the generic and specific roles of thylakoid lipid classes, focusing on their relation with photosynthesis, based on converging evidence from biochemical, biophysical, physiological, genetic and chemical genetic studies. We then detail our current understanding on the dynamic processes that establish and control this very peculiar and essential lipid composition in different biological models, in various physiological contexts and in response to environmental factors.

2. Classes of glycerolipid found in photosynthetic membranes

2.1. Neutral glycolipids: galactoglycerolipids (monogalactosyldiacylglycerol and digalactosyldiacylglycerol)

Galactoglycerolipids are the most abundant lipids in photosynthetic membranes. They comprise two major structures, conserved from cyanobacteria to primary chloroplasts, based on the number of galactose residues in their polar head, i.e. MGDG (1,2-diacyl-3-O-(β-D-galactopyranosyl)-*sn*-glycerol) and DGDG (1,2-diacyl-3-O-(α-

Abbreviations: ATS1, sn-glycerol-3-phosphate acyltransferase; ATS2, 1-acylglycerol-phosphate acyltransferase; DAG, diacylglycerol; DGD1 and DGD2, digalactosyldiacylglycerol synthase 1 and 2; DGDG, digalactosyldiacylglycerol; IEM, inner envelope membrane of the chloroplast; LHCII, light harvesting complex II; MGlcDG, monoglucosyldiacylglycerol; MGD1, MGD2 and MGD3, monogalactosyldiacylglycerol synthase 1, 2 and 3; MGDG, monogalactosyldiacylglycerol; OEC, oxygen evolving complex; OEM, outer envelope membrane of the chloroplast; PA, phosphatidic acid; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; Psb, lumenal extrinsic proteins of the oxygen evolving complex, interacting with photosystem II (includes PsbO, PsbU, PsbV, PsbQ and PsbP); PSI, photosystem I; PSII, photosystem II; Q_A, primary quinone acceptor; Q_B, diffusing quinone; SQDG, sulfoquinovosyldiacylglycerol; WT, wild type

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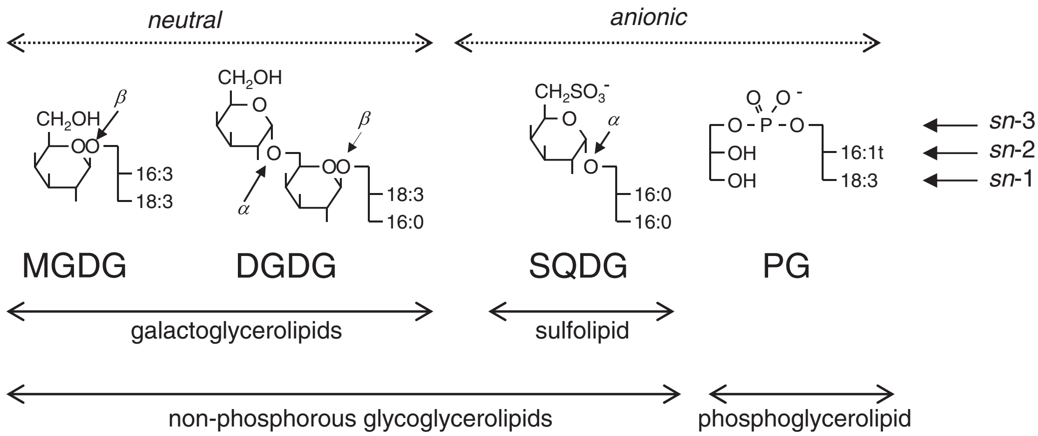

Fig. 1. Main glycerolipid classes conserved in photosynthetic membranes from cyanobacteria to primary chloroplasts of algae and plants. In this illustration of representative lipids from thylakoids of *Arabidopsis* chloroplasts, positions *sn*-1 and *sn*-2 of the glycerol backbone are esterified to fatty acids with 16 or 18 carbon atoms and position *sn*-3 harbors the polar head. MGDG, monogalactosyldiacylglycerol; DGDG, diagalactosyldiacylglycerol; SQDG, sulfoquinovosyldiacylglycerol; PG, phosphatidylglycerol.

D-galactopyranosyl-(1 → 6)-O-β-D-galactopyranosyl)-*sn*-glycerol) [7,8] (Fig. 1). Due to the extensive surface of thylakoids in cyanobacteria, algae and plant cells, MGDG and DGDG constitute the most profuse lipid class on earth [9].

Galactoglycerolipids, and mostly MGDG, are characterized by their high content of polyunsaturated fatty acids. In angiosperms, MGDG contains mostly 16- and 18-carbon ω-3 trienoic acids, i.e. *cis*-7,10,13-hexadecatrienoic acid (16:3) and *cis*-9,12,15-octadecatrienoic acid (18:3) respectively [10]. In algae, MGDG often contains very long chain polyunsaturated acids, with more than 20 carbon atoms and more than 3 double bonds such as eicosapentaenoic acid [11,12]. When present, 16:3 is exclusively at position *sn*-2 of MGDG. In angiosperms, DGDG is mainly 18:3-rich; however, by contrast with MGDG, when a 16-carbon fatty acid is present, DGDG contains mostly the saturated form, palmitic acid (16:0) at position *sn*-1 of the glycerol backbone.

The MGDG/DGDG and galactoglycerolipid/phosphoglycerolipid ratios appear stable, at least in angiosperms, when plants grow under favorable controlled conditions, i.e. when fed with sufficient nutrient sources. This observation supports the existence of a controlled steady state. This steady state was shown to respond to environmental changes. On the one hand, (*i*) environmental stresses that could be detrimental for membrane integrity, like freezing, drought or exposure to ozone, induce the accumulation of additional galactoglycerolipids, i.e. a specific DGDG with a β-galactopyranosyl-(1 → 6)-β-galactopyranosyl polar head instead of the α-galactopyranosyl-(1 → 6)-β-galactopyranosyl polar head and tri- and tetra-galactoglycerolipids in chloroplasts of angiosperms [13–17]. This phenomenon seems to be a recent invention in the evolution of land plants, but will not be discussed in more details in this review. On the other hand, (*ii*) a shortage of phosphate in the environment was shown to trigger a significant increase of the galactoglycerolipid/phosphoglycerolipid ratio, from algae [18] to land

Table 1
Representative glycerolipid compositions of membranes from cyanobacteria and chloroplasts from green algae and angiosperms. The distribution of main glycerolipids is given in percents of total lipid mass. Detected phosphoglycerolipids include PC (phosphatidylcholine), PE (phosphatidylethanolamine), PI (phosphatidylinositol) and PG (phosphatidylglycerol). DPG (diphosphatidylglycerol or cardiolipin), a marker of the contamination by mitochondrial membranes, was below the detection threshold. Conserved glycoglycerolipids consist of MGDG (monogalactosyldiacylglycerol), DGDG (digalactosyldiacylglycerol) and SQDG (sulfoquinovosyldiacylglycerol). MGlcDG (monoglucosyldiacylglycerol) is uniquely detected in cyanobacteria.

	Phosphoglycerolipids					Non-phosphorous glycoglycerolipids			
	PC	PE	PI	DPG	PG	MGlcDG	MGDG	DGDG	SQDG
Membranes from cyanobacteria (*Synechocystis* PCC 6308)[a]									
Envelope and thylakoids	–	–	–	–	11.4	1.7	52	11.7	22
Chloroplasts from green algae (*Chlamydomonas reinhardtii*)[b]									
Envelope membranes	*	4.6	4.1	–	3.5	–	27	31	8
Thylakoids	*	–	2.7	–	6	–	55	20	13
Chloroplasts from angiosperm leaves (*Spinacia oleracea*)[c]									
Envelope membranes									
Total	20	–	4	–	9	–	32	30	6
OEM	32	–	5	–	10	–	17	29	6
IEM	6		1		8	–	49	30	5
Thylakoids	4.5	–	1.5	–	9.5	–	52	26	6.5
Etioplasts from angiosperm (*Pisum sativum*)[d]									
Envelope membranes	17	–	4	–	5	–	34	31	6
Prolamellar body	9	–	2	–	5	–	42	35	6

[a] Present article.
[b] [4].
[c] [5].
[d] [6].
* 21% and 5% of an additional lipid was observed in *Chlamydomonas* in the envelope and thylakoids respectively, initially identified as PC; this phosphoglycerolipid being absent in *Chlamydomonas*, other lipids like DGTS (diacylglyceryltrimethylhomoserine) might be contaminants of envelope preparations.

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