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Review

Evolution of galactoglycerolipid biosynthetic pathways – From cyanobacteria to primary plastids and from primary to secondary plastids

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ABSTRACT

Photosynthetic membranes have a unique lipid composition that has been remarkably well conserved from cyanobacteria to chloroplasts. These membranes are characterized by a very high content in galactoglycerolipids, i.e., mono- and digalactosyldiacylglycerol (MGDG and DGDG, respectively). Galactoglycerolipids make up the bulk of the lipid matrix in which photosynthetic complexes are embedded. They are also known to fulfill specific functions, such as stabilizing photosystems, being a source of polyunsaturated fatty acids for various purposes and, in some eukaryotes, being exported to other subcellular compartments. The conservation of MGDG and DGDG suggests that selection pressures might have conserved the enzymes involved in their biosynthesis, but this does not appear to be the case. Important evolutionary transitions comprise primary endosymbiosis (from a symbiotic cyanobacterium to a primary chloroplast) and secondary endosymbiosis (from a symbiotic unicellular algal eukaryote to a secondary plastid). In this review, we compare biosynthetic pathways based on available molecular and biochemical data, highlighting enzymatic reactions that have been conserved and others that have diverged or been lost, as well as the emergence of parallel and alternative biosynthetic systems originating from other metabolic pathways. Questions for future research are highlighted.

Contents

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1. Introduction

1.1. Galactoglycerolipids are a landmark of oxygen-evolving photosynthetic organisms

Photosynthetic eukaryotes (algae, plants and some protists) are characterized by the presence of a chlorophyll-containing organelle, the chloroplast, whose origin dates back to a primary endosymbiotic event, when an ancestral cyanobacterium was engulfed within or invaded a primary eukaryotic host (for review, [1–8]). The membrane architecture of cyanobacteria and primary chloroplasts are similar: both are delimited by a two-membrane envelope and contain flattened membrane sacs, or thylakoids, in which the photosynthetic complexes are embedded. These membranes have a lipid composition, which has been remarkably well conserved through evolution. In particular, they are characterized by a very high content in galactoglycerolipids, i.e., mono- and digalactosyldiacylglycerol (MGDG and DGDG, respectively). The anomery of the terminal galactosyl groups differs in these two lipids: in MGDG, the galactose is in β conformation, forming the 1,2-diacyl-3-O-(β-D-galactopyranosyl)-*sn*-glycerol structure, whereas in DGDG, the second galactose is in α conformation, forming 1,2-diacyl-3-O-(α-D-galactopyranosyl-(1→6)-O-β-D-galactopyranosyl)-*sn*-glycerol [9,10] (Fig. 1). In this review, we shall refer to these structures as β–MGDG and αβ–DGDG. The transfer of galactose from one galactolipid to another, which occurs in Angiosperms during certain environmental stresses including exposure to ozone or cold, and leading to the production of ββ–DGDG, βββ–triGDG and ββββ–tetraGDG [11,12] shall not be discussed here.

MGDG and DGDG were first isolated from the benzene extract of wheat flour (*Triticum aestivum*) by Carter et al. in 1956 [9]. The systematic inventory of lipids in photosynthetic organisms was initiated a decade later, taking advantage of the thin-layer chromatography separation methods developed by Nichols in 1963 [13] and Allen et al. in 1966 [14]. The ubiquity of galactolipids in all photosynthetic organisms emerged as they were discovered successively in cyanobacteria, e.g., *Anacystis nidulans* and *Anabaena variabilis* [15], various green algae, firstly *Chlorella vulgaris* [16,17] and then *Chlamydomonas reinhardtii* [18,19], various embryophyta (plants), e.g., the moss *Hypnum cupressiforme* [20], the fern *Adiantum capillus-veneris* [21], the gymnosperm *Pinus sylvestris* [22] and the angiosperm *Spinacia oleracea* [23], and eventually to various photosynthetic protists deriving from green algae, such as *Euglena gracilis* [24] or deriving from red algae, such as the diatom *Phaeodactylum tricornutum* [25]. The presence of MGDG and DGDG was recognized as a hallmark of all oxygen-evolving photosynthetic organisms [10], and consequently as the most abundant lipid classes on Earth [26]. Analytical technologies (mass spectrometry, NMR) have increased in sensitivity and throughput the last 15 years. Lipidomic

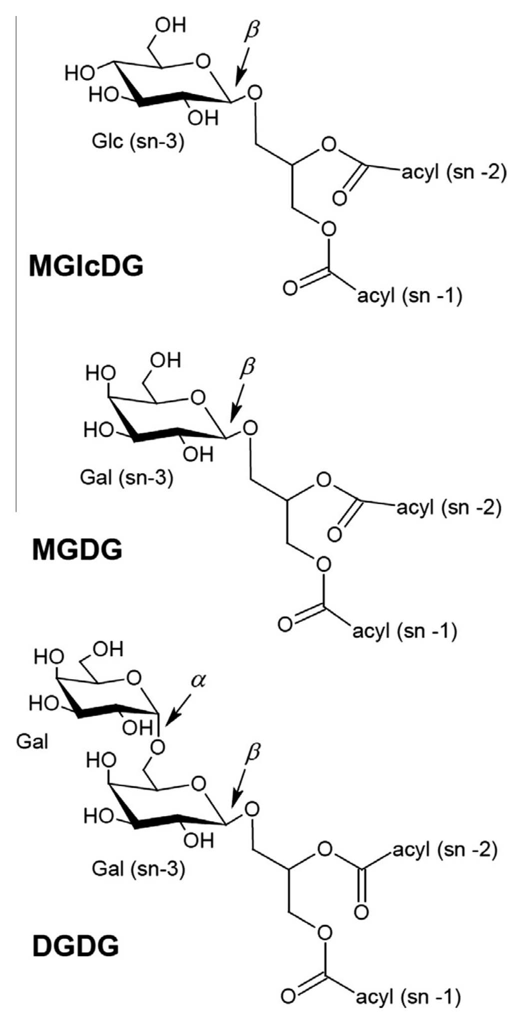

Fig. 1. Galactoglycerolipids conserved in photosynthetic membranes from cyanobacteria to primary chloroplasts of algae and plants. Positions *sn*-1 and *sn*-2 of the glycerol backbone are esterified to fatty acids and position *sn*-3 harbors the polar head. The α and β anomery are indicated. The precursor of galactolipids in cyanobacteria, MGlcDG, is also shown. MGlcDG, monoglucosyldiacylglycerol; MGDG, monogalactosyldiacylglycerol; DGDG, diagalactosyldiacylglycerol.