

Review

# Glycerolipid transfer for the building of membranes in plant cells

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## Abstract

Membranes of plant organelles have specific glycerolipid compositions. Selective distribution of lipids at the levels of subcellular organelles, membrane leaflets and membrane domains reflects a complex and finely tuned lipid homeostasis. Glycerolipid neosynthesis occurs mainly in plastid envelope and endoplasmic reticulum membranes. Since most lipids are not only present in the membranes where they are synthesized, one cannot explain membrane specific lipid distribution by metabolic processes confined in each membrane compartment. In this review, we present our current understanding of glycerolipid trafficking in plant cells. We examine the potential mechanisms involved in lipid transport inside bilayers and from one membrane to another. We survey lipid transfers going through vesicular membrane flow and those dependent on lipid transfer proteins at membrane contact sites. By introducing recently described membrane lipid reorganization during phosphate deprivation and recent developments issued from mutant analyses, we detail the specific lipid transfers towards or outwards the chloroplast envelope.

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**Keywords:** Lipid transfer; Membrane; Plant cell; Vesicle; Membrane contact; Glycerolipid

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**Abbreviations:** CoA, coenzyme A; DAG, diacylglycerol; DGD, DGDG synthase; DGDG, digalactosyldiacylglycerol; DPG, diphosphatidylglycerol; ER, endoplasmic reticulum; MGD, MGDG synthase; MGDG, monogalactosyldiacylglycerol; LTP, lipid transfer protein; LysoPC, lysophosphatidylcholine; PA, phosphatidate; PAP, phosphatidate phosphatase; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PI-TP, phosphatidylinositol transfer protein; PS, phosphatidylserine; SQD, SQDG synthase; SQDG, sulfoquinovosyldiacylglycerol.

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## 1. Introduction

Plant cell membranes contain a wide range of glycerolipids which are not randomly allocated. A selective distribution at the levels of subcellular organelles, membrane leaflets and membrane domains indicates a complex and finely tuned lipid homeostasis. Additionally, the distribution remains relatively well conserved among tissues and plants species (Table 1). In standard plant culture conditions, on one hand, glycolipids, *i.e.* sulfolipid and galactolipids, are restricted to plastid membranes and, on the other hand, phospholipids are the main components of extraplastidic membranes. PE is excluded from plastidic membranes, PC is absent from the inner membranes of chloroplasts and DPG is restricted to mitochondria inner membrane. Sterols and glycosphingolipids are present in plant membranes although in much lower amounts than glycerolipids (for reviews, see [1,2]). Like in mammalian cells, sterols and glycosphingolipids are not homogeneously distributed among membranes and are notably present in the plasma membrane where they are likely involved in membrane domain organization.

In plants, phosphate deprivation has been reported to decrease the phospholipid content, consistent with a mobilization of the phosphate reserve, and conversely to increase non-phosphorous membrane lipids such as DGDG and SQDG [3,4]. Moreover a form of DGDG with specific fatty acids: 16:0 at glycerol sn1 position and 18:2 at sn2 position is especially enhanced [5,6]. Correlated to the lipid composition changes there is also a strong modification of the lipid distribution between membranes. Upon phosphate deprivation, DGDG, a specific plastid lipid in standard conditions, was found in the plasma membrane [7,8], a membranous compartment disconnected from plastid membranes, but dynamically connected to the overall endomembrane system.

Table 1  
Lipid composition of plant cell membranes (in mol% of total) according to [1]

| Membranes            | PC    | PE    | PG  | PI  | PS   | DPG | MGDG | DGDG | SQDG | Sterols | Glyco-sphingolipides |
|----------------------|-------|-------|-----|-----|------|-----|------|------|------|---------|----------------------|
| <i>Endomembranes</i> |       |       |     |     |      |     |      |      |      |         |                      |
| Reticulum + Golgi    | 43–48 | 23–26 | 6   | 6   | 3    |     |      |      |      | 4–15    |                      |
| Tonoplast            | 15–28 | 15–28 | 2   | 5–9 | 2    |     |      |      |      | 14–43   | 12–17                |
| Plasma membrane      | 8–36  | 9–32  | 1–5 | 1–6 | 1–10 |     |      |      |      | 5–60    | 6–30                 |
| <i>Chloroplasts</i>  |       |       |     |     |      |     |      |      |      |         |                      |
| Outer membrane       | 32    |       | 10  | 5   |      |     | 17   | 30   | 6    |         |                      |
| Inner membrane       |       |       | 9   | 1   |      |     | 55   | 30   | 5    |         |                      |
| Thylakoids           |       |       | 7   | 1   |      |     | 58   | 27   | 7    |         |                      |
| <i>Mitochondria</i>  |       |       |     |     |      |     |      |      |      |         |                      |
| Outer membrane       | 52    | 22    | 3   | 10  |      |     |      |      |      | 13      |                      |
| Inner membrane       | 37    | 33    | 2   | 4   |      | 11  |      |      |      | 13      |                      |

Endomembrane analyses are derived from [102–104]. Plastid and mitochondria membrane analyses were done, respectively, by [105,106].

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