

Lipid trafficking: into, within and out of the chloroplast

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Abstract: Plant cellular membranes consist of two different kinds of glycerolipids, phospholipids and galactolipids. The galactolipids make up the bulk of the chloroplast membranes, whereas other membranes such as the plasma membrane, the tonoplast and the endoplasmic reticulum (ER) largely consist of phospholipids. In all plants, the diacylglycerol (DAG) backbones of the chloroplast galactolipids are partially or completely derived from phospholipids synthesised in the ER. Thus, there is a need for transport of phospholipids from the ER to the chloroplast. Evidence is presented and discussed for that the transport of ER-derived galactolipid precursors occurs at sites of physical contact between the chloroplast and a specialised plastid-associated domain of the ER, the PLAM. As galactolipids are synthesised from DAG, there is a need for the enzymatic degradation of ER-derived phospholipids to DAG in the chloroplast envelope. In an *in vitro* system, the degradation of PC to DAG in the chloroplast envelope was found to be mediated by soluble cytosolic phospholipase D and phosphatidic acid phosphatase acting in sequence. Evidence for that the lipid environment of the outer envelope membrane are important for this process is presented. Galactolipids synthesised in the chloroplast envelope are transported across the aqueous stroma to the thylakoid membrane. The evidence at hand suggest that lipid transport from the envelope to the thylakoid is at least partially mediated by vesicles that are formed at the inner envelope and fuses with the thylakoid. This putative vesicular transport system appears to be evolutionary related to vesicle trafficking in the cytosolic secretory pathway. Finally, the effects of phosphate limitation on the lipid composition of oat plasma membranes were studied. Phosphate limitation caused a very large increase in the proportion of the galactolipid digalactosyldiacylglycerol (DGDG) in the plasma membranes; this increase was balanced by a decreased proportion of phospholipids. After four weeks of cultivation in a phosphate-free medium DGDG, a lipid previously assumed to be strictly plastid localised, made up as much as 66 mol% (*sic*) of the root plasma membrane glycerolipids. This finding implies that phosphate limitation causes a massive efflux of DGDG from the plastid to other cellular membranes, such as the plasma membrane. In addition the results also demonstrate a much larger degree of plasticity of plant membrane lipid composition than previously recognised.

Keywords: chloroplast, endoplasmic reticulum, galactolipid, lipid trafficking, phospholipid, plasma membrane, phosphate, thylakoid