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Lipid trafficking at endoplasmic reticulum–chloroplast membrane contact sites

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Glycerolipid synthesis in plant cells is characterized by an intense trafficking of lipids between the endoplasmic reticulum (ER) and chloroplasts. Initially, fatty acids are synthesized within chloroplasts and are exported to the ER where they are used to build up phospholipids and triacylglycerol. Ultimately, derivatives of these phospholipids return to chloroplasts to form galactolipids, monogalactosyldiacylglycerol and digalactosyldiacylglycerol, the main and essential lipids of photosynthetic membranes. Lipid trafficking was proposed to transit through membrane contact sites (MCSs) connecting both organelles. Here, we review recent insights into ER–chloroplast MCSs and lipid trafficking between chloroplasts and the ER.

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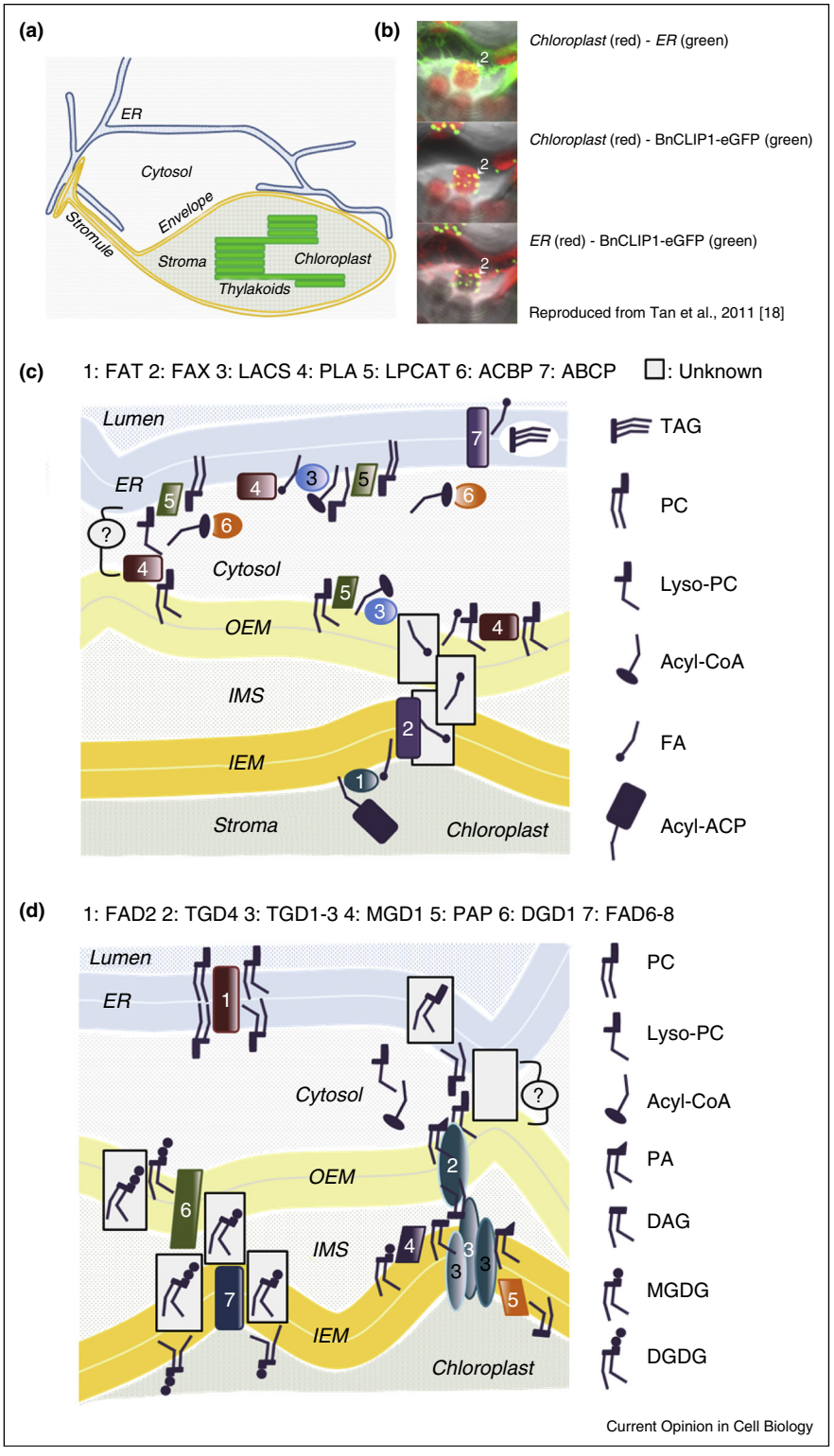
Introduction

The chloroplast, like mitochondrion, is a semiautonomous organelle. It contains an extensive membrane system, the thylakoids, and has a unique lipid composition, where the two galactoglycerolipids, monogalactosyldiacylglycerol (MGDG) and digalactosyldiacylglycerol (DGDG) are essential. Through photosynthesis it achieves the conversion of light energy into chemical energy and produces a diversity of compounds crucial for plant development [1,2]. The chloroplast is the main site of synthesis of fatty acids (FA) which are exported to the endoplasmic reticulum (ER) for phospholipid and triacylglycerol (TAG) synthesis [3–5]. On the other hand, diacylglycerol (DAG), the substrate for galactolipid synthesis which occurs in the chloroplast envelope [5–8], is for a large part generated from phospholipids formed in the ER [9,10]. FA and glycerolipid trafficking between chloroplasts and the ER is therefore very active. However, lipids cannot move freely through the cytosol due to their weak water solubility and except for the import of a limited number of glycosylated proteins from the Golgi, chloroplasts are mostly unconnected with the endomembrane vesicular trafficking network [11]. A few components of the lipid transfer machineries have been identified but most of the transport mechanisms remain to be characterized. The observation of numerous membrane contact sites (MCSs) between chloroplasts and the ER [12,13] lead to the hypothesis that these MCSs could play a role in lipid trafficking [12,14]. We will outline recent results on MCSs and lipid trafficking between chloroplasts and the ER in order to deduce some guidelines for future studies of plant lipid biosynthesis.

General features of the chloroplast–ER membrane contact sites

The ER has a reticulated structure with some cisternae that line up with chloroplasts [13]. By following fluorescent proteins expressed either in the ER or in chloroplasts, it has been observed that some branch end-points of the ER locate at the chloroplast surface [15] and that some thin tubular formations called stromules (stroma-filled tubules) extend from the chloroplast envelope and align along ER tubules, branching accordingly with the ER [16,17] (Figure 1a). Rapid dynamic behavior of stromules suggests a stretch of the chloroplast envelope relying on membrane tethering sites with the ER [17]. Physical association between the ER and chloroplast surface has been demonstrated on isolated *Arabidopsis thaliana* chloroplasts by optical manipulation with laser tweezers [14]. Some ER fragments cannot detach from chloroplasts up to a pulling force of 400 pN, a magnitude relevant with protein–protein interactions. These ER–chloroplast membrane connections have been released from purified chloroplasts by incubation at a lowered pH and have been identified with ER-associated enzyme activities [14]. They were called plastid associated membranes (PLAM). They differ from the chloroplast outer envelope membrane (OEM) by their low galactolipid content and presence of phosphatidylethanolamine (PE) and from the ER by their low glycosylceramide and sterol contents. PE and phosphatidylcholine (PC) are by far the main glycerolipids of PLAM and are equally present [14]. The protein profile of PLAM is also different from the ER and chloroplast envelope [14]. Interestingly, PLAM contains PC synthase but not

Figure 1



Membrane contact sites between chloroplast and endoplasmic reticulum. **(a)** Schematic position of the MCSs reported between chloroplast and ER. MCSs occur along the ER at different sites on the chloroplast surface, either directly with the chloroplast body or along the highly dynamic chloroplast stromules (stroma-filled tubules). The contact surface can extend to a wide area along an ER branch. Both membranes of the chloroplast envelope are present in the MCSs. In the case of stromules extension, initial contact may preferentially locate on the two beaks corresponding to the extreme ends of the chloroplast ovoid form. **(b)** Punctate localization of the lipase BnCLIP1 in overlap areas between