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## Mini-review

New insights on the organization and regulation of the fatty acid biosynthetic network in the model higher plant *Arabidopsis thaliana*Manuel Adrián Troncoso-Ponce<sup>a, b</sup>, Krisztina Nikovics<sup>a, b</sup>, Chloé Marchive<sup>a, b</sup>,  
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## ABSTRACT

In the plastids of plant cells, fatty acid (FA) production is a central biosynthetic process. It provides acyl chains for the formation of a variety of acyl lipids fulfilling different biological functions ranging from membrane synthesis to signaling or carbon and energy storage. The biochemical pathway leading to the synthesis of FA has been described for a long time. Over the last 15 years, and after the genome of the model higher plant *Arabidopsis thaliana* has been sequenced, the scientific community has deployed approaches of functional genomics to identify the actors comprising this pathway. One of the puzzling aspects of the emerging molecular biology of FA synthesis resided in the occurrence of multigene families encoding most enzymes of the pathway. Studies carried out to investigate these families led to the conclusion that most members have acquired non-redundant roles in *planta*. This is usually the consequence of divergent expression patterns of these isogenes and/or of different substrate specificities of the isoforms they encode. Nevertheless, much remains to be elucidated regarding the molecular bases underpinning these specificities. Protein biochemistry together with emerging quantitative proteomic technologies have then led to a better understanding of the structure of the network, which is composed of multiprotein complexes organized within the stromal compartment of plastids: whereas growing evidence suggests that the early steps of the pathway might be associated to the inner envelope membrane, several late enzymes might be localized next to the thylakoids. The question of the existence of a large integrated protein assembly channeling substrates through the whole pathway that would span the stroma remains uncertain. Finally, recent discoveries regarding the post-translational regulation of the pathway open new research horizons and may guide the development of relevant biotechnological strategies aimed at monitoring FA production in plant systems.

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## 1. Introduction

Acyl lipids play crucial roles in many important aspects of plant development and, as such, their agronomical importance hardly needs to be emphasized. First, they are basic components of cellular

membranes and therefore constitute an essential brick of plant architecture. Second, as constituents of the surface layers, they prevent organ fusions and limit both water loss and the entry of pathogenic microorganisms. They also impact on the efficacy of pesticide applications, thereby influencing crop productivity [1]. Third, some plant lipids and their metabolic derivatives participate in various signaling pathways. For instance, jasmonate is known to play an important role in plant-pathogens interactions. Finally, acyl lipids, mainly as triacylglycerols (vegetable oil), are important carbon and energy storage compounds and constitute a key component of both human and livestock diets, which consumption is steeply increasing worldwide [2].

Despite their divergent structures and properties, all these lipids derive from the fatty acid (FA) and glycerolipid biosynthetic pathways [3]. Unlike in other non-photosynthetic eukaryotes, plant de

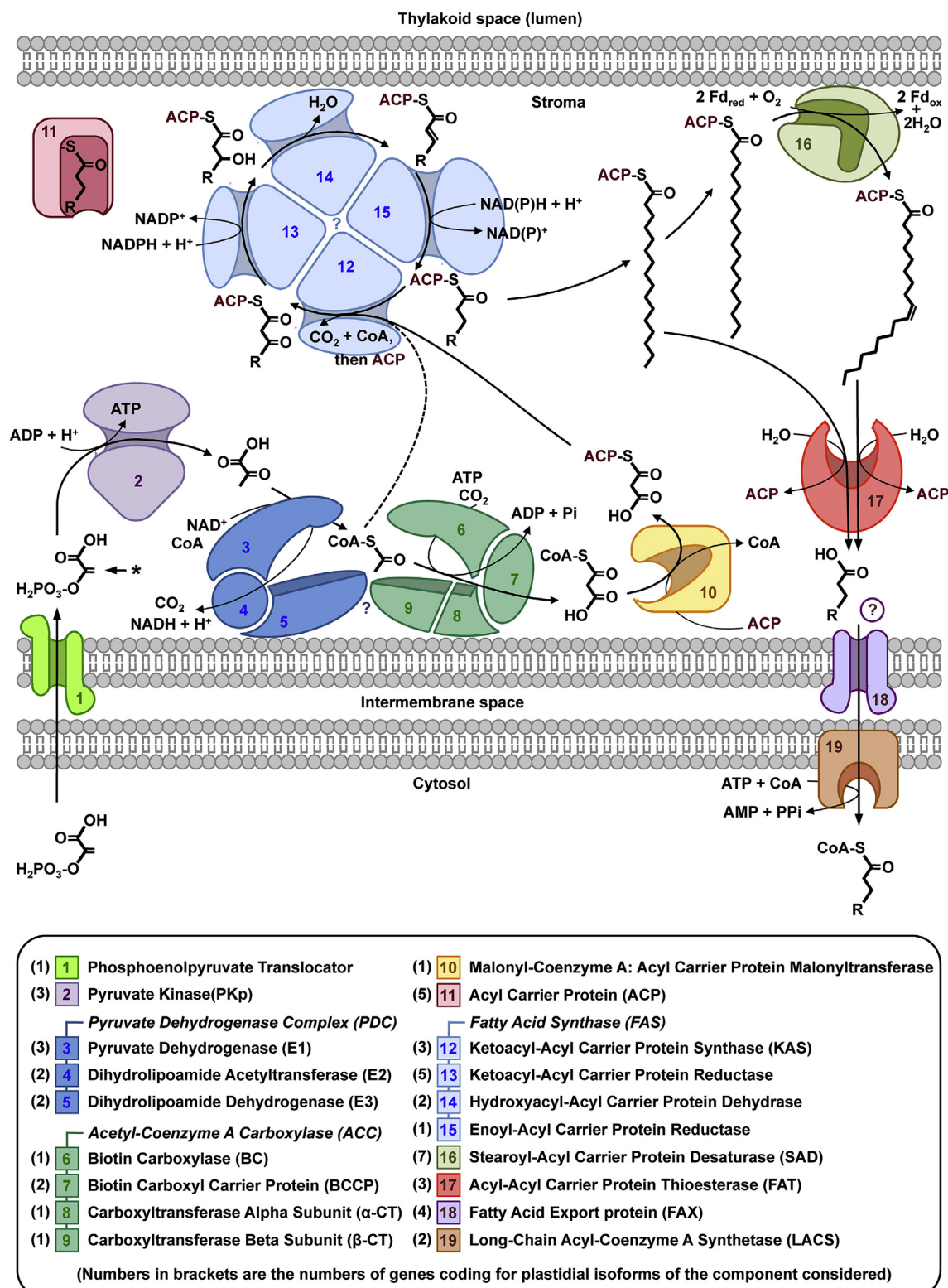
**Abbreviations:** ACC, acetyl-CoA carboxylase; ACP, acyl-carrier protein; BC, biotin carboxylase; BCCP, biotin carboxyl-carrier protein; CT, carboxyltransferase; FA, fatty acid; FAS, fatty acid synthase; FAT, acyl-ACP thioesterase; LACS, acyl-CoA synthetase; SAD, stearoyl-ACP desaturase; PKp, plastidial pyruvate kinase; KAS, ketoacyl-ACP synthase; PDC, pyruvate dehydrogenase complex.

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**Fig. 1.** Schematic of possible organization of the fatty acid biosynthetic pathway in embryo cells of *Arabidopsis thaliana*. Plant *de novo* fatty acid (FA) synthesis occurs in the plastids. Pathways providing substrates to feed in the FA biosynthetic pathway have been extensively reviewed elsewhere [37]. On this simplified scheme, only the main route providing precursors for the formation of FA in embryo cells of *Brassicaceae* species is presented: phosphoenolpyruvate imported from the cytosol {1} is converted into pyruvate by plastidial pyruvate kinases {2}. Supply of phosphoenolpyruvate produced inside the plastid [38] was omitted (\*). Pyruvate is used to generate acetyl-CoA through the action of the pyruvate dehydrogenase complex {3–5}. Since no transport of acetyl-coenzyme A (CoA) between subcellular compartments occurs in plant cells, plastidial acetyl-CoA is the unique building block used for FA synthesis. The first committed step in FA synthesis is the formation of malonyl-CoA from acetyl-CoA by plastidial acetyl-CoA carboxylase {6–9}. Before entering the FA synthesis pathway, the malonyl group of malonyl-CoA has to be transferred from CoA to an acyl carrier protein (ACP) {11}. This transfer is catalyzed by a malonyl-CoA:ACP malonyltransferase {10}. The production of 16- or 18-carbon FA is performed by FA synthase {12–15}, an easily dissociable multisubunit complex consisting of monofunctional enzymes. Whereas some 16:0-ACP is released from the FA synthase machinery, molecules elongated to 18:0-ACP are efficiently desaturated by a stearoyl-ACP desaturase {16}. Long-

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