



Review

Regulation of *de novo* fatty acid synthesis in maturing oilseeds of *Arabidopsis*

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ABSTRACT

As a Brassicaceae, *Arabidopsis thaliana* constitutes an excellent model system to investigate oil biosynthesis in seeds. Extensive tools for the genetic and molecular dissection of this model species are now available. Together with analytical procedures adapted to its tiny seeds, these tools have allowed major advances in isolating and characterising the factors that participate in the metabolic and developmental control of seed filling. Once the biochemical pathways producing storage lipids, namely triacylglycerols, were elucidated, the question of the regulation of this metabolic network has arisen. The coordinated up regulation of genes encoding enzymes of the fatty acid biosynthetic pathway observed at the onset of seed maturation suggests that the pathway may be subjected to a system of global transcriptional regulation. This has been further established by the study of master regulators of the maturation program like LEAFY COTYLEDON2 and the characterisation of the WRINKLED1 transcription factor. These factors have been shown to participate in a regulatory cascade controlling the induction of the genes involved in fatty acid biosynthesis at the onset of the maturation phase. Although much remains to be elucidated, the framework of the regulatory system controlling fatty acid biosynthesis in *Arabidopsis* seeds is coming into focus.

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1. Storage lipids in seeds of *Arabidopsis*

The carbons in fatty acids are highly reduced, so that their oxidation releases twice as much energy as the oxidation of carbohydrates or proteins [1]. Triacylglycerols (TAGs), esters of glycerol and fatty acids, thus constitutes a very efficient form of energy storage. TAGs are accumulated in animal and plant tissues [2]. In seeds, they act as a reserve of carbon and energy allowing to fuel post-germinative seedling growth until seedling photosynthesis can be efficiently established. They also constitute the economic value of seeds in many crops. The model plant *Arabidopsis*

thaliana is closely related to *Brassica napus* (rapeseed), one of the world's major oilseed crops. As such, *A. thaliana* has become a model system for the study of oil synthesis in seeds. This attractive model has often served to provide relatively fast and robust "proof of concept" results before larger investments in crop breeding are made ([3] and references therein).

Seed development can be divided into two main steps: embryo morphogenesis (EM) and maturation. Several studies have been carried out in *A. thaliana* to obtain a complete description of this developmental process [4–7]. EM is initiated by the double fertilisation of the embryo sac that gives rise to the zygote (2n) and endosperm (3n). After a first asymmetrical division of the zygote, the resulting apical and basal cells give rise to the embryo and its suspensor, respectively. Through a series of programmed cell divisions, the embryo acquires the basic architecture of the plant [7,8]. At the end of EM, 6 days after pollination (DAP), the embryo is torpedo shaped. The maturation phase takes place from 7 to 20 DAP and is characterised by the accumulation of storage compounds and the acquisition of dormancy and desiccation tolerance [4,6]. This phase begins with a period of rapid embryo growth allowing the embryo to fill the seed sac while the endosperm is almost totally degraded and reduced to one cell layer surrounding the embryo [9]. This rapid increase in embryo volume is accompanied by the onset of storage compound synthesis. The sustained production of TAGs and seed storage proteins (SSPs) results in a steady increase of seed dry weight (DW) throughout the

Abbreviations: ACP, acyl carrier protein; BC, biotin carboxylase domain; BCCP, biotin carboxyl carrier protein; CT, carboxyltransferase domain; DAGAT, diacylglycerol acyltransferase; DAP, day after pollination; DW, dry weight; EM, embryo morphogenesis; ENR, enoyl-ACP reductase; EREBP, ethylene responsive element-binding protein; FAE, fatty acid elongase complex; FAS, fatty acid synthase; HD, hydroxyacyl-ACP dehydratase; HtACCase, heteromeric acetyl-Coenzyme A carboxylase; KAR, 3-ketoacyl-ACP reductase; KAS, 3-ketoacyl-ACP synthase; LPD, lipamide dehydrogenase; MAT, malonyltransferase; OPPP, oxidative pentose phosphate pathway; PDC, pyruvate dehydrogenase complex; PDH, pyruvate dehydrogenase; PEP, phosphoenolpyruvate; PKp, plastidic pyruvate kinase; PUFA, polyunsaturated fatty acid; SSP, seed storage protein; RuBisCO, ribulose-1,5-bisphosphate carboxylase/oxygenase; TAG, triacylglycerol; VLCFA, very long-chain fatty acid.

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maturation phase. Finally, during the last few days of seed maturation, storage compound synthesis ends while the embryo becomes metabolically quiescent.

The sigmoid pattern of fatty acid accumulation in seeds closely parallels the increase of seed DW, exhibiting a sharp raise between 7 and 17 DAP and a maximal level 18 DAP (Fig. 1). A slight fall of the seed lipid content has been described in several oilseed species including *A. thaliana* at the very end of the maturation process [4,10,11]. This phenomenon most probably illustrates the capacity of the seed to remobilise lipids through β -oxidation prior to germination [12,13]. Once the maturation process is achieved, the

SSPs and TAGs accumulated account for roughly 30–40% of the seed DW each. When analysing the seed composition of 360 *A. thaliana* accessions, the modal oil content is found to be 38% of DW, with most accessions lying within the range 33–43% [14]. Eight fatty acid species are predominantly found in the seeds of *A. thaliana*, namely 16:0, 18:0, 18:1, 18:2 and 18:3 (polyunsaturated fatty acids, PUFAs), 20:0, 20:1 and 22:1 (very long-chain fatty acids, VLCFAs; $C \geq 20$) (Fig. 1). Surprisingly, the seed oil fatty acyl compositions of the different accessions of *A. thaliana* are remarkably conserved, although they originate from different continents and from very different environments [15]. For instance, the proportion of VLCFAs ranges from 13 to 21% of total fatty acids while PUFA content ranges from 53 to 66% of total fatty acids [14]. The dissection of whole mature seeds allows analysing isolated endosperm and embryo tissues separately and reveals that the endosperm accumulates approximately one-tenth of the fatty acids present in whole seeds [16]. The cotyledons of the embryo contain roughly 60% of total fatty acids, and radicle plus hypocotyl the remaining 30% [3]. When comparing the fatty acid composition of these tissues, it appears that all the species detected in the embryo are also present in the endosperm. However, the latter contains proportionally high levels of 16:1, 18:1 and 20:1 ω 7 fatty acids. Around 20% of endosperm fatty acids are n 7 monounsaturated compared with only 2% in the embryo [16]. The fatty acid profiles are different between cotyledons and radicle + hypocotyl as well, the latter exhibiting a higher proportion of 16:0, 18:2 and less 18:3 and 20:1 [3].

TAGs are esters of glycerol in which fatty acids are esterified to each of the three hydroxyl groups of the glycerol backbone. The glycerol molecules are asymmetric in that they do not possess rotational symmetry. As a consequence, each hydroxyl group of the glycerol is biochemically distinct, and the fatty acids are not randomly esterified to them. Stereochemical analyses of the fatty acids in the TAGs of seed oils reveal that saturated species are usually confined to the *sn*-1 and *sn*-3 positions of the glycerol, while unsaturated species occur mainly at *sn*-2 ([1] and references therein). In spite of this segregation of fatty acid species between the *sn* positions of the glycerol, different TAG species can be identified in seed oil [17]. Once synthesised, TAGs are accumulated in subcellular structures called oil bodies. These organelles comprise a matrix of TAGs surrounded by a phospholipid monolayer where the aliphatic chains are oriented to the TAG lumen whereas the phosphate groups are facing the cytosol [18,19]. In dry seeds, cells of the embryo and endosperm are packed full of protein storage vacuoles and oil bodies. It was shown that oil bodies occupy about 60% of the cell volume in the cotyledons of mature embryos. They are preferentially accumulated at the periphery of the cells where they appear to be densely packed [20].

2. The fatty acid biosynthetic network

So far, the small size of *A. thaliana* seeds has prevented to characterise in a detailed manner the organic compounds delivered to the maturing embryos. In seeds of the related *B. napus* species, these compounds mainly consist of sucrose, glucose, Gln, Glu, and Ala [21–23]. Once transported into embryo cells, incoming sucrose can be cleaved via two distinct pathways involving either invertase or sucrose synthase [24–26]. Cleavage of sucrose generates hexose-phosphates that are metabolised through the oxidative pentose phosphate pathway (OPPP) and the glycolytic pathway, providing precursors for fatty acid production in the form of acetyl-CoA. Glycolysis is considered as the predominant pathway for the production of these precursors. In oilseeds, maturing embryos do have a complete glycolytic sequence in the cytosol and in plastids [27–29]. The extent to which both glycolytic sequences are utilised in the conversion of hexose-phosphates into precursors of fatty acid

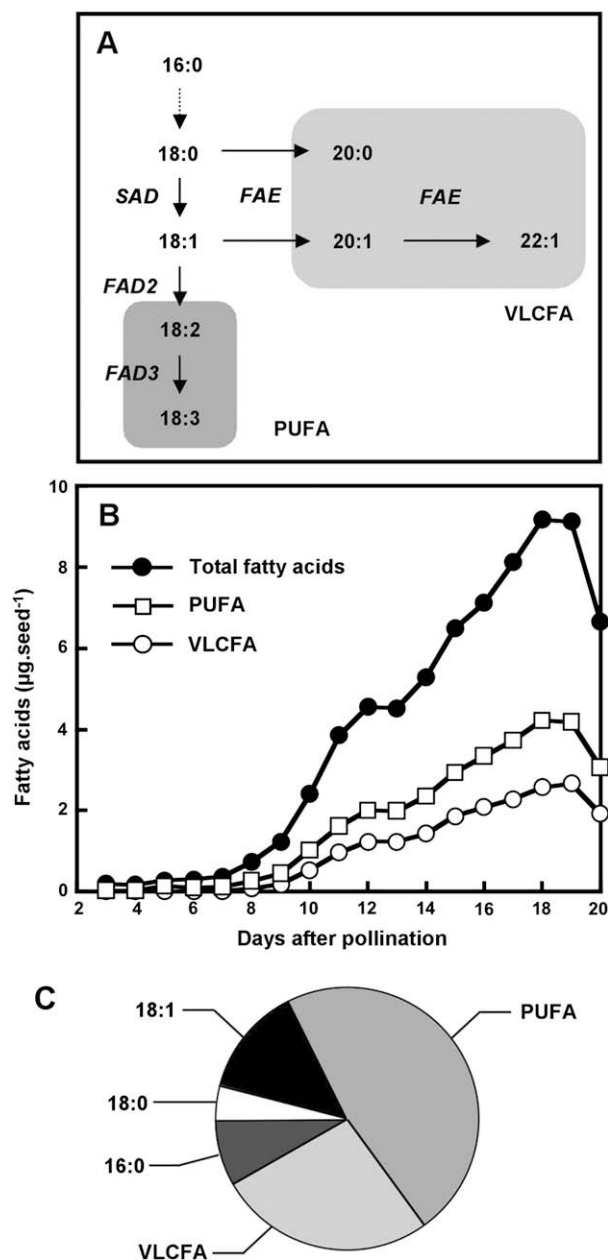


Fig. 1. Oil accumulation in maturing seeds of *Arabidopsis thaliana*. (A) Scheme presenting the most abundant fatty acid species found in seeds of *A. thaliana* together with the pathways of fatty acid synthesis/modification occurring within the Brassicaceae. (B) Fatty acid accumulation in developing seeds of the Wassilewskija accession. (C) Fatty acid composition, in mol%, of mature dry seeds (Wassilewskija accession). FAD2, oleoyl desaturase; FAD3, linoleoyl desaturase; FAE, fatty acid elongase complex; PUFA, polyunsaturated fatty acids; SAD, stearoyl-ACP desaturase; VLCFA, very long-chain fatty acids.

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