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A comparison of natural and induced diversity in plant oils☆

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Abstract – Currently, there is a growing demand to replace the compounds in a given product that are of a petroleum origin with renewable resources. One of these compounds, called fatty acid (FA), is the main component of vegetable oils. FA composition is not only responsible for the physicochemical properties of plant oils, but it also determines their uses. For example, since time immemorial, products containing lipids have been used for lighting and heating purposes. They are also excellent lubricants and possess drying properties important molecules for painting, and wood preservation. In terms of nutrition, they have a high-energy content, are part of our daily health requirements, and are used for animal feed. We present here some lipids of interest, the plants that produce them naturally with high yield, the enzymes responsible for their synthesis when known, and their possible uses, as well as resources and ways that could allow the lipids of interest to be produced in quantity in different hosts.

Keywords: diversity / oleaginous plants / seeds / seed oil / biosynthesis / fatty acids

Résumé – Une comparaison de la diversité naturelle et induite dans les huiles végétales. Actuellement, il existe une demande croissante pour remplacer les composés d'origine pétrolière d'un produit donné par des ressources renouvelables. Depuis des temps immémoriaux, les produits contenant des lipides sont utilisés pour l'éclairage et le chauffage. Ils sont également d'excellents lubrifiants, possèdent des propriétés siccatives importantes pour la peinture, la préservation du bois. En termes de nutrition, ils ont un contenu énergétique élevé, font partie de nos besoins quotidiens en matière de santé ainsi que pour l'alimentation humaine et animale. Nous présentons ici quelques lipides d'intérêt, les plantes qui les produisent naturellement avec un rendement élevé, les enzymes responsables de leur synthèse lorsqu'elles sont connues, leurs utilisations possibles, ainsi que les ressources et les moyens qui pourraient permettre de produire en quantité les lipides d'intérêt dans différents hôtes.

Mots clés : diversité / plantes oléagineuses / graines / huile de graines / biosynthèse / acides gras

1 Introduction

World production of vegetable oils (2019–2020 crop year) is estimated at more than 200 million T[1], 74% of which is used mostly for human nutrition and 5% for animals, with the remaining 20% used for energy purposes or chemistry. The plant kingdom, rich with more than 350 000 angiosperm species, represents an immense reservoir of unexploited natural product diversity, but only a very small number of plant species (palm, soybean, rapeseed, sunflower, coconut, etc.) are cultivated, and their oil is extracted mainly from fruits or seeds. Only a few dozen among the hundreds of different FAs produced and stored in plant oils are exploited for different uses.

During the last 50 years, databases specifically dedicated to plant lipids have been developed. The lipid content of thousands of vegetable oils can be scrutinized using websites providing easy access to multiple databases. One online scientific database is Cyberlipid[2] whose purpose is to collect, study and diffuse information on all aspects of lipidology. Seed oil fatty acids, or SOFA[3], the oldest database and hosted by the Max Rubner-Institute (Karlsruhe, Germany), is a collection of the FA composition of wild plant seeds from the appropriate

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[1] http://www.statista.com/

[2] http://cyberlipid.gerli.com/

[3] https://plantfadb.org/

pharmaceutical, botanical and chemical literature (Aitzetmüller *et al.*, 2003). This database was the first to permit exploration of about 580 different FA structures, the composition from more than 7000 plant species, and lists about 130 000 individual percentage data for FA occurring in plant seeds. PlantFAdb[4] (previously PhyloFAdb) (Ohlrogge *et al.*, 2018) provides updates and enhancements to SOFA, and allows users to search and display FA composition data for over 9000 plants. It also includes more than 17 000 tables from more than 3000 publications and hundreds of unpublished analyses. All these databases represent valuable and unique tools to explore FA diversity in plants, chemotaxonomic relationships between FA structures, and plant species by displaying these relationships on dynamic phylogenetic trees (Aitzetmüller *et al.*, 2003; Ohlrogge *et al.*, 2018). The PlantFAdb catalogs just over 2% of the estimated species in the plant kingdom, with representative seed compositions for most phylogenetic clades available; thus a number of FAs remains to be discovered in seeds (Cahoon and Li-Beisson, 2020). Included in this database are also relatively ancient sets of data. Practical resources for exploring the diversity of plant lipids are also provided by valuable books (Gunstone *et al.*, 1986; Ucciani, 1994).

In the following sections, we review a selection of FAs and focus our attention on the plants that contain the most FAs, as well as the enzymatic systems involved in their synthesis, when known. At the end, we give examples of oils from plants, some of which are already cultivated, and which have unique properties due to their content in specific FAs.

We also present examples of plants whose oil production has been modified by modern genome techniques such as gene expression modification and genome editing (CRISPR Cas9). As a complement to modern techniques we end by suggesting some possible ways to better exploit biodiversity, and try to identify some underlying challenges.

2 Biosynthesis and accumulation of oils with FAs of interest: from enzymes to plants that produce them naturally and in large quantity

Sugars are synthesized by plants through photosynthesis and converted into a variety of storage compounds, including oils (Baud, 2018). The main compounds of oil are FAs which are esterified to a glycerol skeleton. In plants, oil synthesis requires the collaboration of different metabolic pathways and subcellular compartments. The *de novo* synthesis of FAs requires malonyl-coenzyme A (CoA) which is the carbon donor, an acyl bound to an acyl carrier protein (ACP), and various cofactors. FA synthesis occurs in the plastids and is carried out by an enzyme complex, with four monofunctional proteins, termed fatty acyl synthase (type II FAS), which catalyzes cycles of successive reactions. It begins with a Claisen condensation between the acyl-ACP and a malonyl-ACP (3C, product from pyruvate oxidative decarboxylation) catalyzed by three β-ketoacyl-ACP synthases isoforms: KASIII up to 4C-ACP, KASI up to 16C-ACP, and KASII catalyzes the last elongation up to 18C-ACP. The addition of two C requires the participation of three additional enzymes.

3-ketoacyl-ACP reductase (KAR) catalyzes a ketone hydrogenation, 3-hydroxyacyl-ACP dehydratase (HAD) catalyzes water elimination and enoyl-ACP reductase (ENR) catalyzes the hydrogenation of the alkene. Each synthesis cycle uses one malonate (3C) and results in the elongation of acyl-ACP by 2C (Baud and Lepiniec, 2010; Li-Beisson *et al.*, 2010). Simultaneously in the chloroplast, elongation of FAs occurs until stearic acid (18:0) (Fig. 1.1). Stearoyl-ACP desaturase (SAD) desaturates stearic acid (18:0) bound to ACP into oleic acid ($18{:}1^{\Delta 9}$) bound to ACP. SAD, a Δ9 acyl-ACP desaturase (Fig. 1.2), is a plastid-localized non-membrane-bound soluble desaturase which contains a di-iron center (Lindqvist *et al.*, 1996). Similarly, Δ9 acyl-ACP desaturase transforms palmitic acid (16:0) bound to ACP into palmitoleic acid ($C16{:}1^{\Delta 9}$) bound to ACP (Fig. 1.3). Acyl-ACP thioesterases from TE14 family (Swarbrick *et al.*, 2020), located at the inner plastid envelope membrane, hydrolyze the newly formed acyl-ACP into free FA and ACP (Fig. 1.4). Free FAs, the chain length for which is dictated by enzyme specificity of acyl-ACP thioesterases, are transported through the membrane and are activated into the form of CoA esters by long-chain acyl-CoA synthetases (LACS) (Fig. 1.5) and transferred to the endoplasmic reticulum (ER) by acyl-CoA binding proteins (Fig. 1.6), feeding the eukaryotic pathway responsible for the formation of phospholipids, triglycerides, and other neutral lipids.

Different enzymatic systems further modify FAs through catalyzing sequential reactions in the ER, using FA belonging to different metabolic pools, such as acyl-CoA, phosphatidylcholine (PC), or GL as substrates. FAD2 (Δ12 desaturase) transforms oleic acid bound to PC into linoleic acid ($18{:}2^{\Delta 9c,12c}$) bound to PC (Fig. 1.7) (Zeng *et al.*, 2017). FAD3 catalyzes the desaturation of linoleic acid bound to PC ($18{:}2^{\Delta 9c,12c}$) acid into $18{:}3^{\Delta 9c,12c,15c}$ bound to PC (Fig. 1.8) (Arondel *et al.*, 1992). FADX, a fatty acid conjugase desaturase and a divergent form of Δ12 oleate desaturase FAD2, are responsible for the synthesis of the conjugated eleostearic acid ($18{:}3^{\Delta 9c,11t,13t}$) (Fig. 1.9) (Dyer *et al.*, 2002). Structurally, unrelated enzymes that have evolved separately are cytochrome P450 and delta 12 epoxygenase (Δ12 desaturase-like). These enzymes are capable of catalyzing the synthesis of 12-epoxy vernolic acid ($\Delta 12{,}13\text{–}O\text{–}18{:}1^{\Delta 9c}$) by using PC-bound $18{:}3^{\Delta 9c,12c,15c}$ as substrate (Fig. 1.10) (Cahoon *et al.*, 2002).

Homologs of FAD2 are also capable of hydroxylating the Δ12 position of PC bound oleic acid (van de Loo *et al.*, 1995), producing ricinoleic acid ($\Delta 12\text{–}OH\text{–}18{:}1^{\Delta 9c}$) (Fig. 1.11). An activated form of ricinoleic acid, ricinoleoyl-CoA enters a discontinuous elongation process in which the 3-hydroxy C20 intermediate (not shown) is elongated into nebraskanic ($7{,}18\text{–}(OH)2\text{–}24{:}1^{\Delta\text{-}15}$) by a specialized FAE (Li *et al.*, 2018) (Fig. 1.12).

The synthesis of very long chain fatty acids (VLCFAs, longer than 18C), is catalyzed in the ER by the fatty acid elongase (FAE) complex which uses malonyl-CoA and long-chain acyl-CoA as substrates. The pool of long chain acyl-CoA is probably resulting from exchange of FAs between the acyl-

[4] https://plantfadb.org/

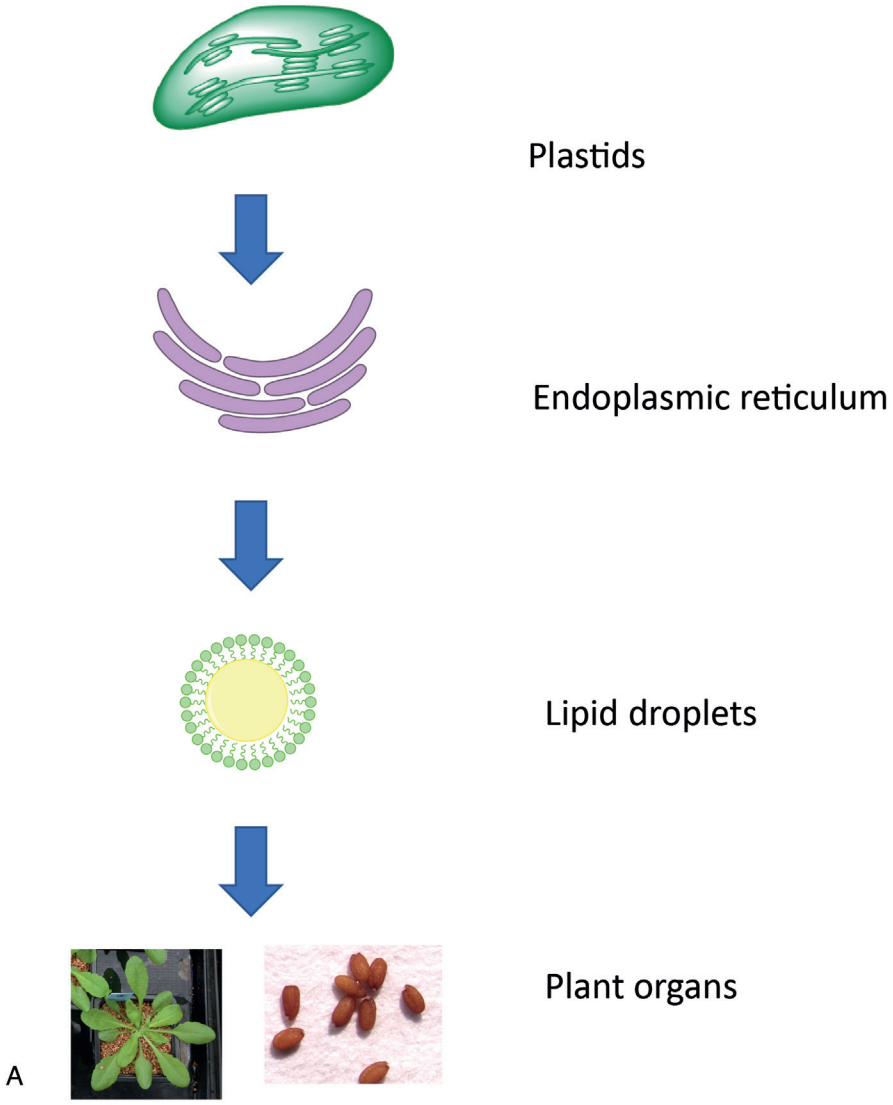
Plastids
Endoplasmic reticulum
Lipid droplets
Plant organs
A

Fig. 1.

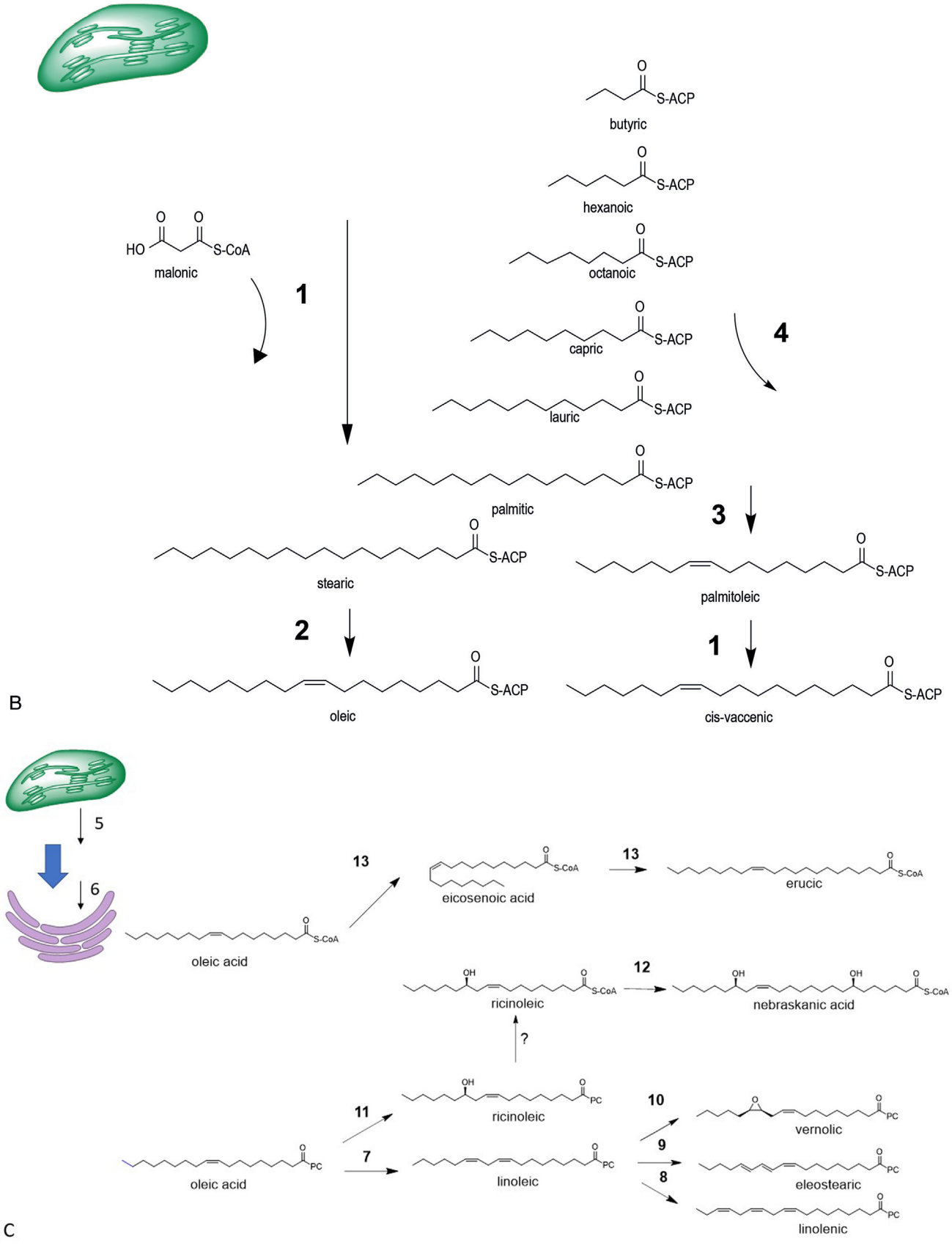

Fig. 1. (Continued)

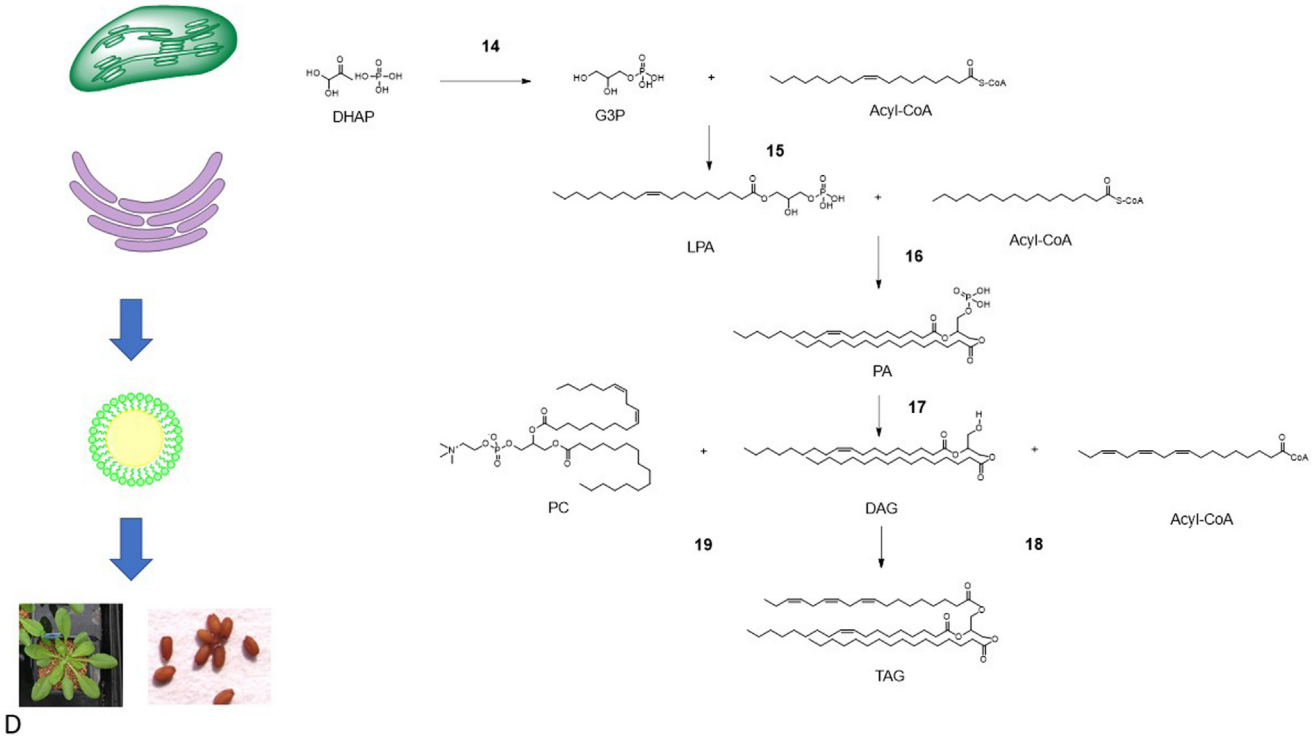

Fig. 1. Overview of biosynthesis, accumulation, and deposition of selected fatty acids in plants.
Panel A: In plants, synthesis of neutral lipids requires the collaboration of plastids and the endoplasmic reticulum while their accumulation occurs in ER derived organelles called lipid droplets, found in all organs. Blue arrows indicate flux toward neutral lipid accumulation in organelles and selected organs. **Panel B**: The synthesis and elongation of FAs, bound to ACP occur in the chloroplast till 18:0 (**1**, fatty acyl synthase) and its desaturation into $18{:}1^{9c}$ by 9 stearoyl-ACP desaturase (SAD) (**2**). In a similar way, 16:0 desaturation by 9 palmitoyl-ACP desaturase (PAD) (**3**) produces palmitoleic acid ($16{:}1^{9}$), which can be further elongated to produce cis vaccenic acid $18{:}1^{11c}$, (**1**). The synthesis of Acyl-ACP can be interrupted Acyl-ACP thioesterases (**4**) releasing free FA with chain lengths under 18C. **Panel C:** Free FAs are transported through the membrane, activated into the form of CoA esters by long-chain acyl-CoA synthetases (LACS) (**5**) and transferred to the endoplasmic reticulum (ER) by acyl-CoA binding proteins (**6**), where they are further processed. Oleic acid elongation and the other FA modifications take place mostly in the ER and involve different enzymes (elongases, hydroxylases, desaturases) which use acyl bound to ACP, glycerolipids (GL), PC and acyl-CoA as substrates. Oleic acid bound to PC or GL is transformed into linoleic acid (**7**, 12 desaturase). FAD3 catalyzes the desaturation of linoleic ($18{:}2^{9c,12c}$) acid into linolenic ($18{:}3^{9c,12c,15c}$) (**8**). FADX, a fatty acid conjugase desaturase is responsible for the synthesis of eleostearic acid ($18{:}3^{9c,11t,13t}$) (**9**). Vernolic acid (12,13–O–$18{:}1^{9c}$) is obtained upon the action of cytochrome P450 on 5 PC-bound linolenic acid or of delta 12 epoxygenase (12 desaturase like) (**10**). Hydroxylation of the 12 position of PC bound oleic acid (fatty acid hydroxylase) by homologs of fatty acid desaturase 2 (FAD2) (**11**) produces ricinoleic acid (12–OH–$18{:}1^{9c}$). Ricinoleoyl-CoA, deriving from Ricinoleoyl-PC, is transformed into nebraskanic (7,18–(OH)2–$24{:}1^{-15}$) acid upon the action of hydroxylases (**12**). Elongation of oleoyl-CoA by acyl-CoA elongase (**13**) produces eicosenoic ($20{:}1^{11c}$) and erucic acid ($22{:}1^{13c}$). **Panel D:** Esterification of FA to glycerol for accumulation into lipid droplets. Dihydroxyacetone phosphate (DHAP) originates from glycolysis and is converted to glycerol-3-phosphate (G3P) by glycerol-3-phosphate dehydrogenase (G3PDH) (**14**). G3P is acylated at *sn1* positions by a glycerol phosphate acyltransferase (GPAT) (**15**) which produces lysophosphatidic acid (LPA). Acylation at *sn2* position by a 1-acyl G3P acyltransferase (**16**) produces phosphatidic acid (PA). The dephosphorylation of PA by phosphatidic acid phosphatases (PAP) (**17**) produces 1,2-diacyl-*sn*-glycerol (DAG). Another acyl group is esterified at the *sn-3* position of DAG either by acyl-CoA:1,2-diacyl-*sn*-glycerol acyltransferase (DGAT, acetyl-CoA dependent pathway) (**18**), or by the phospholipid:1,2-diacyl-*sn*-glycerol acyltransferase (PDAT) (**19**) which transfers acyl from PC to DAG. For the sake of clarity, we have focused our attention on the FAs which are exemplified in this review. For more detailed and comprehensive descriptions of FA metabolism in model plants and crops, please refer to the following very recent articles (Baud, 2018; Cahoon and Li-Beisson, 2020; Miklaszewska *et al.*, 2021).

CoA and PC pools due to the action of lysophosphatidylcholine acyltransferase (LPCAT) (Stahl *et al.*, 2008). FAE catalyze reactions similar to those occurring during *de novo* FA synthesis in the plastids (Haslam and Kunst, 2013). FAE which encodes the β-ketoacyl-CoA synthase is responsible for elongation of oleic acid (18:1) activated under the form of CoA ester to eicosenoic acid (20:1) (Fig. 1.13) and further to erucic acid (22:1) (Fig. 1.13) (Barret *et al.*, 1998; Li *et al.*, 2012).

The enzymatic esterification of FA to various molecules containing OH groups (glycerol, sterols, alcohols) leads to four different compounds: phospholipids, sterol esters, triacylglycerols (TAG), and waxes. Phospholipids are mostly used to build up membranes, while sterol esters and TAG are stored in specialized organelles called lipid droplets (Huang, 2018), and waxes which cover the epidermal cells.

TAG synthesis results from successive acylations of glycerol-3-phosphate (G3P). The conversion of dihydroxyacetone phosphate (DHAP), originating from glycolysis to glycerol-3-phosphate (G3P) is catalyzed by glycerol-3-phosphate dehydrogenase (G3PDH) (Fig. 1.14). G3P is sequentially acylated at *sn*1 and *sn*2 positions by a glycerol phosphate acyltransferase (GPAT) (Shockey *et al.*, 2016) (Fig. 1.15) which produces lysophosphatidic acid (LPA), and by lysophosphatidic acyltransferase (LPAAT) (Maisonneuve *et al.*, 2010) (Fig. 1.16) which produces phosphatidic acid (PA). The dephosphorylation of PA by phosphatidic acid phosphatases (PAP) (Fig. 1.17) produces 1,2-diacyl-*sn*-glycerol (DAG). Another acyl group is esterified at the *sn*-3 position of DAG either by acyl-CoA:1,2-diacyl-*sn*-glycerol acyltransferase (DGAT, acetyl-CoA dependent pathway) (Fig. 1.18), or by the phospholipid:1,2-diacyl-*sn*-glycerol acyltransferase (PDAT) (Fig. 1.19). which transfers acyl from PC to DAG to catalyze the production of TAG in the acetyl-CoA-independent pathway (Zhang *et al.*, 2009).

WRINKLED1 (WRI1) transcription factor is encoded by a gene belonging to the APETALA transcription factor family. While it has been found that mutant *wri*1 can cause an 80% reduction in seed oil content (Focks and Benning, 1998), recently, WRI1 has been shown to be a key regulator of genes involved in late glycolysis and FA biosynthesis in *Arabidopsis thaliana* seeds, and also in crops (Baud *et al.*, 2007; Maeo *et al.*, 2009; Li *et al.*, 2015).

Among the more than 450 FA known in the plant kingdom, five FAs are termed usual, palmitic acid (16:0), stearic acid (18:0), oleic acid ($18:1^{\Delta 9c}$), linoleic acid ($18:2^{\Delta 9,12c}$), and α-linolenic acid ($18:3^{\Delta 9,12,15c}$) (Li-Beisson *et al.*, 2013). These are found in biological membranes, so mostly in phospholipids. The vast majority of FAs are stored in triacylglycerol (Cahoon and Li-Beisson, 2020), in plant polymers such as cutin and in waxes, and represent most of the diversity of these molecules, and are termed unusual. The asymmetric distribution of usual and unusual FAs between the different compartments without a doubt reflects the strong selection pressure exerted by evolution on biological membranes. The structure of FAs includes the number of carbon atoms in the acyl chain, and the presence of various modifications (unsaturation, hydroxylation, epoxidation, and cyclopropane groups). This structure governs the physical-chemical properties of FAs, and gives them very different reactivities, which makes them unique, renewable raw materials for chemistry (Metzger, 2009). Table 1 details the chemical formula, together with some properties and uses of selected usual and unusual FAs found in large quantities in the oil of cultivated and non-cultivated plants.

2.1 Lauric acid (12:0)

Palm kernel oil contains high amounts of octanoic (8:0), capric acid (10:0), and lauric acid which are extracted from the endosperm of the palm oil (up to 38.7%) (Dussert *et al.*, 2013). Lauric acid in its sulfated form, is an ingredient found in many household products (toothpaste, shampoos, shaving foams, and bubble baths) (Vandeputte, 2012). Its global market was estimated at ~5 million T in 2015[5], and strongly depends on the cultivation of palm trees. The accumulation of FAs with defined alkyl chain length is under the control of acyl carrier protein (ACP) thioesterases (Jones *et al.*, 1995). These enzymes release free FAs, thus terminating alkyl chain elongation, and permitting esterification of the glycerol skeleton. Large amounts of octanoic, capric and lauric acid (up to 94.4, 93.8, and 85.9) are found in the oils of different cuphea shrub species. Cuphea is a *Lythraceae* common in tropical countries (Graham and Kleiman, 1992). A specialized diacylglycerol acyltransferase contributes to the extreme medium-chain FA content of cuphea oil (Iskandarov *et al.*, 2017). However, despite the report of 93.8% capric content in seeds from *Cuphea avigera var pulcherrima* (Graham and Kleiman, 1992), the cultivation of this plant remains impaired by poor yield, seed shattering, and indeterminate growth (Zanetti *et al.*, 1993).

2.2 Myristic acid (14:0)

Pycnanthus Kombo (African nutmeg) is a Magnoliaceae which can reach 15–20 m in size. Its drupes are rich in oil (up to 58%), with a high myristic acid content (14:0) (61.6%) (Banerji *et al.*, 1984), making it an important source of oil and wax for fabricating candles, soap, fuel, and lubricants (PROTA)[6] (van der Vossen and Mkamilo, 2007).

2.3 Palmitic acid (16:0)

Native to the coast and coastal plains of southeastern North America, the fruit of the shrub *Myrica carolinensis* accumulates up to 29% oil rich in palmitic (77.5%) and myristic (21.5%) acids (Harlow *et al.*, 1965). Different derivatives of palmitate are used as emollients or plasticizers, and can be used to fabricate candles.

Thus, plants belonging to different botanical families capable of producing oils highly enriched in non-saturated FAs with up to (16:0) are found in nature. They represent alternatives to palm trees, and do not seem to be cultivated in large areas, or even domesticated. Key enzymes involved in the accumulation of specific FAs in these plants have, to our knowledge, not always been identified.

[5] https://www.transparencymarketresearch.com/sodium-lauryl-sulfate-market.html

[6] https://www.prota4u.org/database/

Table 1. Fatty acids of interest cited in this manuscript, some uses, and plants showing the highest content in their oil.

Fatty acid common name	Nomenclature	Plant with highest known content (%)	Family	Uses	Reference
Octanoic	8:0	*Cuphea pulcherrima* (94.4%)	*Lythraceae*	Perfume, antifungal	(Graham and Kleiman, 1992)
Capric	10:0	*Cuphea koehne (93.8%)*	*Lythraceae*	Flavors, perfumes, dyes	(Graham and Kleiman, 1992)
Lauric	12:0	*Actinodaphne hookeri (96%)*	*Lauraceae*	Detergent	(Banerji *et al.*, 1984)
Myristic	14:0	*Pycnathus kombo (61.6%)*	*Myristicaceae*	Candles, soap, fuel, lubricants	(Banerji *et al.*, 1984)
Palmitic acid	16:0	*Myrica carolinensis (77.5%)*	*Myricaceae*	Plasticizer	(Harlow *et al.*, 1965)
Palmitoleic	$16:1^{\Delta 9}$	*Doxhanta unguis (> 60%)*	*Bignoniaceae*	Production of octene	(Nguyen *et al.*, 2010)
Stearic	18:0	*Momordica charantia (74.5%)*	*Cucurbitaceae*	Candles, soap, detergents	(Dave *et al.*, 1985)
Vaccenic	$18:1^{\Delta 11c}$	*Entandraphragma (62%)*	*Meliaceae*	Production undecanoic acid (11:0, Nylon production)	(Kleiman and Payne-Wahl, 1984)
Vernolic	Δ12,13–O–$18:1^{\Delta 9c}$	*Vernonia galamensis (79–81%)*	*Asteraceae*	Adhesives, varnish, paintings, solvent	(Ucciani, 1994)
Ricinoleic	Δ12–OH–$18:1^{\Delta 9c}$	*Ricinus communis (90%)*	*Euphorbiacee*	Polymers	(Gunstone *et al.*, 1986)
Eleostearic	$18:3^{\Delta 9c,11t,13t}$	*Vernicia fordii (75.2%)*	*Euphorbiaceae*	Varnishes	(Zhang *et al.*, 2014)
Linolenic	18:3cis-$^{\Delta 9,12,15}$	*Fragaria vesca (43%)* *Linum usitatissimum (35–66%)* *Euphorbia niciciana (74.3%)* *Vitis vinifera (63–75.7%)*	*Rosaceae* *Linaceae* *Euphorbiaceae* *Vitaceae*	Food, paintings, plastics	(Johansson *et al.*, 1997; Ucciani, 1994)
Erucic	$22:1^{\Delta 13c}$	*Crambe abyssinica (55–60%)*	*Brassicaceae*	Emolients, tensio actifs	(Ortiz *et al.*, 2020)
Nebraskanic Wuhanic acid	7,18–(OH)2–$24:1^{\Delta 15}$ 7,18–(OH)2–$24:2^{\Delta 15c,21c}$	*Orychophragmus violaceus (38%)*	*Brassicaceae*	Lubricant	(Romsdahl *et al.*, 2019)

2.4 Stearic acid (18:0)

Momordica charantia, a Cucurbitaceae, also called bitter gourd, accumulates up to 30% oil with a high stearic acid (18:0) content (74.5%) (Dave *et al.*, 1985). The performance of this plant cultivated in Asia, Africa and in the Caribbean is remarkable when compared to sunflowers possessing two mutations. One of these is Es1 (the sunflower stearoyl-ACP desaturase [SAD named SAD17]), which cannot accumulate more than 50% stearate (Salas *et al.*, 2021), and its oil must be refined before use.

2.5 Oleic acid ($18:1^{\Delta 9c}$)

Oleic acid ($18:1^{\Delta 9c}$) results from the desaturation of stearic acid (18:0) by Δ9 stearoyl-ACP desaturase, a chloroplastic enzyme (Fig. 1). Several examples of oleic acid uses for synthesis of chemicals are given in (Metzger, 2009), and high oleic sunflower has been commercialized since 1984 (Purdy, 1986).

FAs may be further elongated and modified by specific enzymes, mostly in the ER and contributes to the oil's useful properties for various uses. In the following sections, we detail selected examples of oils enriched in FA obtained after modifications of oleic acid ($18:1^{\Delta 9c}$).

2.6 Erucic acid ($22:1^{\Delta 13c}$)

Erucic acid is a long chain unsaturated FA accumulated in high erucic acid rape (HEAR), and its synthesis is under the control of the BnFAE1 gene (*Brassica napus* fatty acid elongase). This gene encodes the β-ketoacyl-CoA synthase responsible for the elongation of oleic acid (18:1) to eicosenoic acid (20:1) and further to (22:1) (Barret *et al.*, 1998; Li *et al.*, 2012). Erucic amide, a compound commonly used as a slip additive in the plastic industry, results from the condensation of erucic acid with ammonia. Cross-pollination of HEAR with food quality rapeseed (*i.e.*, canola that does not produces erucic acid) could result in the production of oil with altered

quality. Thus, these two plants must be distantly cultivated. *Crambe abyssinica*, a Brassicaceae, also naturally produces an oil with a high erucic acid content (Samarappuli *et al.*, 2020) and could be an alternative crop.

The use of a gene stacking strategy is necessary to achieve a substantial increase in the amount of erucic acid in Crambe seed oil. First, it involves the expression of *Limnanthes douglasii* lysophosphatidic acid acyltransferase (LPAAT) (Cao *et al.*, 1990) to compensate for the inability of the endogenous LPAAT to use erucoyl-CoA as an acyl donor. A second gene is expressed, *B. napus* BnFAE1 (fatty acid elongase), which encodes the β-ketoacyl-CoA synthase, and is responsible for elongation of FAs from oleic acid ($18:1^{\Delta 9c}$) to eicosenoic acid ($20:1^{\Delta 11c}$) and further to erucic ($22:1^{\Delta 13c}$). In the end, FAD2 encoding a fatty acid desaturase catalyzing the desaturation of oleic ($18:1^{\Delta 9c}$) to linoleic acid ($18:2\ ^{\Delta 9c,12c}$), is down-regulated (Li *et al.*, 2012). Taken together, these modifications lead to a decrease of oleic, linoleic and linolenic ($18:3^{\Delta 9,12,15}$) acid and permits a substantial increase in erucic acid ($22:1^{\Delta 13c}$), from 55–60% in the wild type seeds (Ortiz *et al.*, 2020) to 73% in the best *C. abyssinica* transgenic line obtained by the authors (Li *et al.*, 2012).

2.7 Ricinoleic acid (Δ12–OH–18:$1^{\Delta 9c}$)

Castor seeds (*Ricinus communis*) contain 39–59% of an oil rich (83–90%) in ricinoleic acid (Δ12–OH–$18:1^{\Delta 9c}$) (Gunstone *et al.*, 1986). Castor fatty acid 12-hydroxylase (RcFAH12) (Fig. 1), a homolog of (FAD2) is the enzyme that hydroxylates the Δ12 position of PC bound oleic acid (van de Loo *et al.*, 1995), producing ricinoleic acid. Castor oil has for a long time been used as lamp oil, an ingredient for cosmetics, as a purgative, and more recently as a lubricant (Dumeignil, 2012). Castor oil also serves as the basis for the synthesis of many compounds, such as polyamide 11 (Rilsan), an agro-based bioplastic that is used in the hoses of the automotive industry (Winnacker and Rieger, 2016), and was classified as a strategic material critical to the US national defense by the Agricultural Materials Act P.L. 98-284 passed by Congress in 1984. Despite the industrial interest in castor oil, the poisons contained in the plant, as well as in many *Euphorbiaceae*, still represent a roadblock to its cultivation. The plant is not really cultivated in Europe; however approximately 1 443 588 T of castor seeds were produced in 2019 in India, the world's largest producer (82% of world production).

2.8 Vernolic acid (Δ12,13–O–18:$1^{\Delta 9c}$)

The seeds of various Asteraceae, such as *Vernonia galamensis* a plant native to East Africa, *Stokesia laevis*, native to the USA, or *Crepis biennis*, a plant commonly found in France, produce oils enriched (79–81%) in an epoxy FA called vernolic acid (Δ12,13–O–$18:1^{\Delta 9c}$) (Ucciani, 1994). The seeds of *Euphorbia lagascae*, a Euphorbiaceae, also accumulate in their oil up to 63% vernolic acid (Cahoon *et al.*, 2002), due to the action of a cytochrome P450 on PC-bound linoleic acid (Cahoon *et al.*, 2002). *S. laevis* epoxidase exhibits high homology with *V. galamensis* epoxygenase, and transforms linoleic acid into vernolic acid (Hatanaka *et al.*, 2004). The genetic transformation of soybean by the *S. laevis* epoxidase gene together with *V. galamensis* diacylglycerol acyltransferase permits accumulation of up to 17.6% vernolic acid in the seeds (Li *et al.*, 2010). The high content in the epoxy groups (68% vernolic acid) of vernonia oil permits its use in the manufacturing of industrial adhesives, varnishes, paints, and coatings (Baye *et al.*, 2005).

2.9 Linolenic acid ($18:3^{\Delta 9,12,15c}$)

Flax seeds contain 35–50% of an oil rich in linolenic acid ($18:3^{\Delta 9,12,15c}$) (35–66%) that is responsible for its drying properties. Two genes (LuFAD3A, LuFAD3B) that encode a flax seed microsomal desaturase capable of desaturating linoleic acid into linolenic have been identified and characterized (Vrinten *et al.*, 2005) (Fig. 1). Historically, oxidized flax seed oil was used for the synthesis of well-known linoleum flooring. In 2014, 2.6 million tons of flax seeds were produced worldwide, with 16 000 T produced in France alone. This country imports these seeds, mostly for food purposes (Labalette *et al.*, 2011). Seeds belonging to other botanical families may also contain significant amounts of linolenic acid. The performance of *Euphorbia niciciana*, not cultivated yet, seems to exceed that of flax, with similar to higher seed oil (39–44%) or linolenic acid (74–76%) content (SOFA) (Ucciani, 1994). As already stated; Euphorbiaceae notoriously accumulate toxic compounds in seeds and vegetative tissues, hindering their exploitation. Strawberry (Fragaria, Rosaceae) seeds represent around 1% of the fruit weight (Grzelak-Blaszczyk *et al.*, 2017) and their oil contains up to 43% linolenic acid (Johansson *et al.*, 1997). Strawberry production was 12 106 585 T in 2019[7], and, so more than 121 065 T seeds were potentially available and could provide 52 058 T of linolenic acid. Grape seeds are rich in linolenic acid (63–75.7%) (Ucciani, 1994). California generates about 435 449 T/year of grape pomace, and a recent techno-economic assessment estimates the annual production of 1627 T of grape seed oil (Jin *et al.*, 2021).

2.10 Eleostearic acid ($18:3^{\Delta 9c,11t,13t}$)

Vernicia fordii tree, a Euphorbiaceae tree accumulates in its seeds an oil called tung oil. Native to Asia, it was introduced to South America, Thailand, and the southern United States, where due to climatic hazards, cultivated areas have fallen sharply (Zhang *et al.*, 2014). The consecutive action of two desaturases (FAD2 and FADX) converts PC-bound oleic acid into linolenic and eleostearic acid ($18:3^{\Delta 9c,11t,13t}$), a conjugated trans trienoic acid (Dyer *et al.*, 2002) (Fig. 1). Tung oil is easily oxidized due to its very high content in eleostearic acid, up to 75% (Zhang *et al.*, 2014), and is commonly used in formulations of inks, dyes, coatings, and resins because of its drying properties (Sonntag, 1979). 588 190 T of tung nuts were produced worldwide, mostly by China and Brazil (50% of 2019 world production, FAO). Production of oeleostearatic acid is not limited to Euphorbiaceae. As an example, *Momordica charantia*, a Cucurbitaceae is also capable of accumulating up to 56% eleostearic acid (Ucciani, 1994) in its seeds. As the plant is cultivated in the tropical Asian region, precise statistics about its cultivation are not available (PROTA). More examples of plants accumulating eleostearic acid have been reported (Hennessy *et al.*, 2016), such as *Punica granatum (pomegranate)*, and *Fevillea trilobata (cucurbitale)*.

[7] http://www.fao.org/faostat/en/

3 Lipid accumulation in organs other than seeds

Seeds and fruits are not the only organs that accumulate lipid. The use of tubercules from *Cyperus Esculentus* as food has been discovered in ancient Egypt (Vega-Morales *et al.*, 2019). It has also been suggested that there were even earlier uses by hominids who lived in East Africa between 2.4–1.4 million years ago, who survived mainly on a diet based on grasses and Cyperaceae sedges (Macho, 2014). *C. Esculentus* produces an oil (17–29.%) (Wang *et al.*, 2020) rich in oleic acid (58.8%) (Ucciani, 1994) and is cultivated in several countries (Vega-Morales *et al.*, 2019). *Tetraena mongolica* Maxim is a Zygophyllaceae found in inner Mongolia (China). Due to the high TAG content of the vegetative parts, and as the stems contain about 46 mg TAG/g dry matter (Wang *et al.*, 2007), this plant was used as firewood.

4 Plants producing oils with low viscosities

As already stated, the oils used for food, health, chemistry, and energy are extracted from a very small number of plants when compared to existing diversity. The vast majority of oils have been characterized with analysis of FAs derivatives (generally methyl esters) using gas chromatography. The number of FAs contained in these oils is very small in comparison to the usual and unusual FAs, and the positional distribution of FAs on the glycerol skeleton remains largely unknown, except for oil from crops.

The use of classic TLC or more elaborate nuclear magnetic resonance techniques allows for the detection of unknown FA or new esterified FA that could provide an explanation for the low viscosity of oil. Members of the genus Lesquerella, are Brassicaceae known to be rich in hydroxy FAs. The analysis of TAG structure revealed the presence of molecules containing two or more acyl groups joined *via* ester linkages between an −OH moiety on the hydrocarbon chain of one acyl group and the −COOH moiety of another acyl group, termed estolides (Hayes *et al.*, 1995). *Orychophragmus violaceus* (Chinese violet Cress) is a Brassicaceae originating from China used for ornamental purposes. The seed oil was believed to be rich in linoleic acid, until the discovery of two major components, C24 FAs containing hydroxyl groups at carbon atoms 7 and 18, and the deciphering of a new pathway for the biosynthesis of hydroxyl FAs (Li *et al.*, 2018). A premature or "discontinuous" elongation of a 3–OH intermediate by a divergent 3-ketoacyl-CoA synthase during a chain extension cycle explains the origin of the presence of dihydroxy FAs in *O. violaceus* (nebraskanic and wuhanic acids) (Li *et al.*, 2018) (Fig. 1). *O.s violaceus* oil contains up to 38% nebraskanic and wuhanic acids, and its coefficient of friction for the sliding steel surfaces at 100 °C is three times lower in comparison with castor oil (Li *et al.*, 2018). The biosynthetic basis for estolides in *O. violaceus* seeds remains unknown (Cahoon and Li-Beisson, 2020).

The seed of the plant *Euonymus alatus*, a flowering shrub in the Celastraceae family (also called winged spindle or burning bush), contains around 44% oil (Earle, 1966) composed of more than 90% 3-acetyl-1,2-diacylglycerol (also termed acetyl TAGs). *E. alatus* accumulates oil specifically in the albumen and the embryo of seeds. This plant grows mostly in gardens for ornamental purposes, and the question of its industrial cultivation has not yet been considered. Developments in nucleic acid sequencing techniques allowed for the identification of an acyltransferase that is both expressed in the genesis of *E. alatus* albumen (Durrett *et al.*, 2010) and involved in accumulation of acetyl TAGs. Acetyl TAGs possess a low viscosity and can be used either directly as fuel or as lubricants of renewable origin.

5 Transformation of plants

Many plants that synthesize interesting oils possess characteristics that are unfavorable to their cultivation (low yield, presence of toxins, some are invasive species). Crop engineering offers solutions to overcome these issues.

5.1 Achieve competitive yields

Crops modified by transgenic techniques can accumulate oils that approach the level and quality of native plants. The efficient accumulation of oils with a given composition relies on the expression of enzymes synthesizing specific FAs, as well as on the availability of acyl transferases and acyl acceptor molecules. The biosynthesis and accumulation of lipids requires the collaboration of several metabolic pathways and branches, as well as different compartments and even possibly TAG remodeling. Because these requirements are complex, efficient lipid engineering is very difficult (Bates, 2016; Bhandari and Bates, 2021). Only a small number of studies have shown that modifying the expression of a single gene is enough to significantly improve the oil content and nature of seeds. To achieve this goal, additional specific genes usually need to be expressed in order to both synthesize FAs and to accumulate them efficiently in target organs.

Leaves represent targets for increasing oil accumulation using the concepts of FA synthesis ("Push"), TAG assembly ("Pull"), and lipid turnover ("Protect") (Vanhercke *et al.*, 2014). The next section presents successful examples of this concept.

The synthesis of TAGs requires a glycerol backbone, acyl acceptor on which the FAs will be esterified. Increasing the availability of reaction precursors will increase the final yield of TAG synthesis. Glycerol 3-phosphate dehydrogenase allows the transformation of dihydroxyacetone phosphate into glycerol 3-phosphate (G3P) (Push), the first substrate for TAG synthesis. Expression of foreign acyl carrier protein (ACP) thioesterases modifies the availability of specific FAs for esterification on the glycerol backbone and these enzymes are also targeted (Push). WRINKLED1 (WRI1), transcription factors are involved in transcriptional regulation for adapting the rate of acyl chain production to cell requirements (Push) (Vanhercke *et al.*, 2014).

DGATs are classified into three distinct classes, sharing no sequence homology, and probably result from convergent evolution. DGAT1 and 2 types are integral membrane proteins of the endoplasmic reticulum (Stone *et al.*, 2006; McFie *et al.*, 2010). In *A. thaliana*, AtDGAT1 makes a major contribution to seed oil content (Routaboul *et al.*, 1999). In crops producing

non-edible oils, members of the DGAT2 family incorporate unusual FAs containing hydroxy- (*Ricinus communis*) and epoxy groups (*V. galamensis*) into seed TAGs (Kroon *et al.*, 2006; Li *et al.*, 2010). DGAT3 are soluble proteins (Saha *et al.*, 2006; Chi *et al.*, 2014) and the *A. thaliana* isoform possesses a [2Fe–2S] cluster (Ayme *et al.*, 2018). Due to the slow velocity of the catalyzed reaction, DGAT has been regarded as a limiting step in TAG accumulation at the time of high lipid synthesis during oil accumulation and seed maturation in *B. napus* (Perry and Harwood, 1993). Efficient incorporation of unusual FAs into TAG not only requires enzymes specific for their production but also the expression of DGATs, which selectively use them (Bates *et al.*, 2014). Recent results obtained upon expression of one DGAT3 isoform from *Camelina sativa* demonstrated the high DGAT activity of the enzyme upon expression in leaves and its preference for unsaturated FAs (Gao *et al.*, 2021). This makes DGAT3 a promising candidate for increasing both oil yield (Pull) and quality in plants. DGATs from different families thus represent a reservoir of enzymes allowing the incorporation of specific FAs into TAGs.

Two different research teams have overexpressed yeast glycerol 3-phosphate dehydrogenase (*gdp*1) in different plants, alone or in combination with DGAT1 from *A. thaliana* (Pull). In oilseed rape, overexpression of *gdp*1 increased the amount of G3P available for acylation by successive acyltransferases, resulting in a 40% increase in the lipid content of the mature seed (Vigeolas *et al.*, 2007). Oleosins are the major proteins found at the surface of LDs, which are oil storage organelles. The role of oleosins in lipid accumulation (Protect) was demonstrated in seeds (Siloto *et al.*, 2006), and more recently in leaves (Zhai *et al.*, 2021). The co-expression of three genes involved in different aspects of TAG production; WRI1 (Push), DGAT1 (Pull), and OLEOSIN (Protect) permitted the accumulation of more than 15% TAG (dry weight basis) *in Nicotiana tabacum* leaves (Vanhercke *et al.*, 2014). More details about TAG metabolism and accumulation in plant vegetative tissues are extensively detailed by Xu and Shanklin (2016).

Seeds from *C. sativa* co-expressing the *A. thaliana DGAT1* and yeast *gdp*1 accumulate up to 13% higher oil content and up to 52% higher seed mass compared to wild-type plants (Chhikara *et al.*, 2018). Similarly, co-expression of specific acyltransferases and acyl-ACP thioesterases (Wiberg *et al.*, 1997; Iskandarov *et al.*, 2017) in Brassicaceae improved the accumulation of medium-chain saturated FAs in the seeds.

Plant oils containing ω-7 FAs have potential as sustainable feedstocks. However, plants with oil containing a very high content (> 60%) of palmitoleic acid (*Doxhanta unguis* or *Kermadecia sinuate*) are not cultivated and even considered as invasive (*D. unguis*). Using a strategy, consisting of strongly suppressing KASII (elongase activity) and increasing the desaturase activity in the host plant, two teams were able to obtain plants that accumulate high quantities of ω-7 FAs in seeds. Amounts are around 2–3% in *A. thaliana* and *C. Sativa* wild-type plants. Transgenic *A. thaliana* accumulate up to 71% ω-7 FAs, (levels equivalent to those found in Doxhanta seeds (71.9%) (Nguyen *et al.*, 2010) and transgenic *C. sativa* 44.3% (Rodriguez-Rodriguez *et al.*, 2021).

Euonymus alatus diacylglycerol acetyltransferase (*Ea*DAcT) was cloned and expressed in different plants (Arabidopsis, Camelina, Soya). As a consequence, it was found that wild type *A. thaliana* plants expressing *Ea*DAcT accumulated 45% acetyl-TAGs in their oil (Durrett *et al.*, 2010). Expression of *Ea*DAcT in plants affected the expression of DGAT1, the enzyme limiting TAG accumulation, permitting the accumulation of up to 70% acetyl TAG in camelina and soybean. In transgenic camelina, grown in the field, with the silenced DGAT1 gene and expressing *Ea*DAcT, it was found that the oil contained up to 85% acetyl TAG (Liu *et al.*, 2015a).

5.2 Accounting for undesired effects

Seeds store lipidic compounds in their reserves, which act as energetic molecules and/or building blocks for the establishment of autotrophic plantlets. The modification of the nature and quantities of accumulated lipids can affect the fate of seeds sometimes with unexpected or even deleterious effects of which we give some examples.

Transgenic rice plants engineered to overproduce linoleic acid have been developed by different research groups. Plants overexpressing delta-12 fatty acid desaturase have unexpectedly shown enhanced cold tolerance during the reproductive stage and an increase of grain yield (46%) under cold conditions (Shi *et al.*, 2012). Similarly, overexpression in rice of an ω-3 fatty acid desaturase from *Glycine max* (GmFAD3A) has been shown to enhance the total polyunsaturated FAs (PUFAs) content in seeds, as well as seed germination rate at low temperature (Wang *et al.*, 2019).

Although inactivation of rapeseed stearoyl-acyl-desaturase has resulted in increased production of stearic acid in Brassica seeds (up to 40%) compared to conventional varieties, the transgenic seeds have shown poor germination rates (Knutzon *et al.*, 1992). A similar situation was observed in *A. thaliana* seeds where the high amounts of stearate (up to 25%) were negatively linked to germination performance (Kazaz *et al.*, 2020). In genetically transformed *Brassica juncea*, a negative correlation between seed stearate content (up to 31%) and seed germination performance was also observed (Bhattacharya *et al.*, 2015).

6 GM crops improved for oil traits

6.1 Cultivated

GM crops have been cultivated in the field for more than twenty years. In 2018 the surface planted with these crops was 184 million hectares total (Brookes and Bargfoot, 2020), mostly located in different countries outside of the European Union. In 2016, most GM crops grown had traits that allowed them to resist herbicides or insect (Napier *et al.*, 2019); however, there are other aspects of oil crops to consider.

Because of their composition, oils can have beneficial or deleterious effects for consumers, whether they are humans or animals. Coriander seed oil (CSO) is highly enriched in petroselenic acid, and in a scientific opinion, the European Food Safety Authority (EFSA) panel concluded that the novel food ingredient, CSO, was safe under the proposed uses and use levels (Agostoni *et al.*, 2016) as a food supplement for healthy adults. Since the presence of erucic acid in rapeseed oils can be harmful to the heart muscle, varieties with little or no erucic acid have been developed, and EFSA has issued a

scientific opinion on the daily intake level for erucic acid (Knutsen *et al.*, 2016).

A search performed using the International Service for the Acquisition of Agri-biotech Applications (ISAAA) website[8] indicates that at least three crop plants (*B. napus*, *Carthamus tinctorius*, *Glycine max*) with traits improved for oil amount or composition using GM techniques are commercially available. It should be noted that modified plants can accumulate FAs that they do not naturally synthesize. For example, *B. napus* expressing *Umbellularia californica* 12:0-ACP thioesterase are intended for palmitic acid production. When considering the accumulation of DHA, seven foreign genes (desaturases and elongases) are expressed in other events. To achieve the production of docosapentaenoic acid (C22:5n-3), a FA not naturally found in plants, the introduction of ten foreign genes was necessary. Modifications of *Carthamus tinctorius* L. are available as well, in which the synthesis of delta-12 desaturase enzyme is suppressed by RNA interference, or in which the production of FATB enzymes or acyl-acyl carrier protein thioesterases are suppressed by RNA interference.

6.2 Camelina, an emerging crop, capable of synthesizing and accumulating non-plant FA

Given that some modified plants have already been successfully grown in the field, *C. sativa* represents an excellent example of a plant for which seed oil can be improved using modern techniques (transformation, gene edition).

C. sativa is a hexaploid and possesses three delta-12-desaturase (FAD2) genes. Using similar approaches based on CRISPR-Cas9 gene editing, (Morineau *et al.*, 2017; Jiang *et al.*, 2017) performed selectively targeted mutation of the three FAD2 genes. Both teams obtained transgenic Camelina lines with lipid profiles, ranging from 10% to 62% oleic and 16% to over 50% oleic acid in their seeds. High oleic acid content was associated with a decrease of polyunsaturated FAs.

Camelina plants expressing *Ea*DAcT were grown in the field and produced up to 70 mol% acetyl-dioleoyl-glycerol. The overall features (seed weight, oil content, seed yield, and harvest index) of camelina accumulating acetyl-TAG were not modified (Liu *et al.*, 2015b). A camelina construct was also designed to accumulate in its seeds eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), FAs not naturally present in plants. Camelina has now been evaluated in the field, in separate geographic and regulatory locations (the UK, US, and Canada). Its ability to grow in the field, accumulating EPA and DHA only in its seeds confirms the promise of this modified plant as a new source of omega-3 rich oils normally found only in marine organisms (Han *et al.*, 2020).

7 From the rationale exploration to the uses of biodiversity

Compared to other organs, seeds store the widest repertoire of FAs in their oil, and the number of accumulated FA species certainly exceeds the 580 found in the SOFA database. The plants listed in PlantFAdb (over 9000) represent a small fraction of the plant kingdom (over 350 000 different species), even if most phylogenetic clades have representative seed compositions. Thus, a large number of unusual FAs and their assemblies into glycerolipids remains to be discovered in seeds, and even in other organs. Further esterifications of acyl chains can lead to networks of FAs, increasing the number of molecules potentially produced and stored in oils in a combinatorial manner. Approaches using combinations of liquid chromatography (LC) and mass spectrometry (MS) are very efficient and allow for the identification of many molecules. In addition to the already cited examples of the detection of nebraskanic and wuhanic acids in (Li *et al.*, 2018), an analysis of the leaf lipidome has also yielded 393 molecular species within 23 different lipid classes (Tarazona *et al.*, 2015) that cannot be deduced from the FA composition alone. A very recent article (Gan *et al.*, 2022) report on the exploration of Thunbergia genus, which revealed that numerous species accumulate petroselenic ($18{:}1^{\Delta 6}$) instead of sapienic acid ($16{:}1^{\Delta 6}$). Thus, detailed study of a genus may reveal the accumulation of unexpected FAs, resulting from probable evolutionary divergence in the genus.

The databases cited here represent useful tools to identify plant species storing unusual FAs. The 1000 plants (oneKP or 1KP) initiative[9] is an international multi-disciplinary consortium that has generated large-scale gene sequencing data for over 1000 species of green plants (Leebens-Mack *et al.*, 2019). The exploitation of this sequence database permits the exploration of genomes to identify candidates' genes involved in the synthesis of these FAs and their assembly in the form of neutral lipids. To efficiently use these databases, difficulties arise in linking and integrating the different levels of data (genomic, transcriptomic, lipidomic) that can be used to identify the genes or metabolic pathways involved in the biosynthesis of specific FAs for further metabolic engineering. Many enzymes that allow the accumulation of original FAs in seed oils remain to be discovered that would allow these compounds to be accumulated in plants whose metabolic pathways have been altered.

Biotechnology approaches, including gene editing, have led to convincing and fairly rapid results in terms of modification of the FA composition of oils. In all cases, these approaches should not be excluded from the exploration and the better use of existing plants, whether cultivated or found in existing commercial collections, botanical gardens, or even in the wild.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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[8] https://www.isaaa.org/

[9] https://sites.google.com/a/ualberta.ca/onekp/

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