African Journal of Biotechnology Vol. 7 (25), pp. 4743-4749, 29 December, 2008
Available online at http://www.academicjournals.org/AJB
DOI: 10.5897/AJB08.034
ISSN 1684–5315 © 2008 Academic Journals

Review

Key mediators modulating TAG synthesis and accumulation in woody oil plants

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Accepted 27 November, 2008

Woody oil plant is gaining increasing interest as substitute for petroleum-derived materials, and its enriched hydroxy and conjugated fatty acids for industrial applications. In pursuit of high-value and level oils, a better understanding of mechanisms regarding triacylglycerol (TAG) synthesis and accumulation is required. Here we first summarized the germplasm resources of woody oil plants, and the key mediators on TAG synthesis and accumulation, among which diacylglycerol acyltransferases (DGATs) is discussed for its clear role in TAG amount and composition. Furthermore TAG-accosiated proteins called oleosins are also discussed in depth due to their determination on the amount and size of oil bodies. Previously, two transcripts of oleosins were isolated from *Vernicia fordii* by us, and the homology of oleosins is analyzed. TAG accumulation is the result of multi-play action of the above mediators at varied levels. Furthermore, the channel of fatty acids flux also serves as a limiting factor for determination of the rate of TAG accumulation. The knowledge of key mediators modulating TAG accumulation will provide new insight on further metabolic engineering of oilseeds in woody plants.

Key words: Woody oil plant, triacylglycerol accumulation, diacylglycerol acyltransferases, oleosin, fatty acid flux.

INTRODUCTION

As a result of reducing petrochemical resources and environmental consciousness, there will be a worldwide increasing demand for oil plants and their derivatives as substitutes for petrochemicals in industrial applications, such as biolubricants, biofuels, nylon precursors and detergent feedstocks (Metzger and Bornsheuer, 2006). According to international biodiesel standard, oils from woody oil plants have been defined as biodiesel materials, such as oils from *Camellia oleifera*, *Jartropha curcas*, *Elaeis guineensis*, etc. and others supply natural oil for industrial usage, such as *V. fordii, Keteleeria evelyniana, Pinus koraiensis*, etc. So far, tremendous application on crops and model plants has been performed for the production of biofuel feedstocks and oleo-chemicals. For example, soybean seeds are currently used for biodiesel production (Hill et al., 2006). Compared with oil crops, the woody oil plants relatively hold considerable superiority in two aspects. Firstly, wood oil plants will not have competition with foodstuff and have no danger about food contamination. Secondly, woody plants enriched oils can produce novel fatty acid for industrial usage and feedstocks for biodiesel. However, the woody plants generally have limiting agronomic traits such as low yields, toxicity and the very limited geographical growing areas. Fortunately, genetic engineering offers an exciting opportunity. With a particular focus on woody oil plants oilseed, we review the woody oil plant resources and the key mediators on TAG complex process of synthesis and accumulation.

It is well-known that three biosynthetic events are involved in the production of seed storage oils. The first is the fatty acids synthesis in plastids. The second refers to these fatty acids modification by enzymes located in the endoplasmic reticulum (ER). The third is the packaging of the fatty acids into TAG, which subsequently accumulate in oil bodies that bud off from the ER. The paper sets out to discuss the complex process of TAG synthesis and accumulation in woody plants at molecular level. In addition, environmental effect and carbon supply on accumulation were also taken into account.

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WOODY OIL PLANTS ARE ATTRACTIVE FOR ITS USAGE

Woody oils plants are utilized for many food and industrial applications. They include edible oils, processed ingredients for the food industry and feedstocks for chemicals such as formulation of paints, inks, resins, vanish, plastics and biodiesel production. Table 1 summarized woody oil plants resources in the world.

KEY ENZYMES ON NOVEL FATTY ACID MANIPULATION IN WOODY OIL PLANTS

The constituent fatty acids in TAG confer specificity and selectivity of oil usage. Through metabolic engineering of the fatty acid composition, it is possible for woody oil plants to supply petroleum-derived materials in fuels, lubricants, and special chemicals. After fatty acids synthesis, there is an important process of manipulation, in which desaturases are active. They generally include Δ^9 and Δ^{12} desaturase and their various homologs. Recent researches have been focused on divergent forms of the Δ^{12}-oleic acid desaturase (FAD2-like enzyme). Divergent FAD2 forms catalyzed a wide range of fatty acid modification, including conjugation, hydroxylation and epoxygenation (Iwabuchi et al., 2003; Cahoon and Kinney, 2005). For instance, α-eleostearic acid (18:3 $\Delta^{9cis,\ 12cis,\ 15cis}$) in *V. fordii* (tung tree) is catalyzed by Δ^{12} fatty acid conjugase FADX (Dyer et al., 2002). FAD2-like conjugase from *punicia granatum* (pomegranate) for punicic acid has also been described (Hornung et al., 2002; Iwabuchi et al., 2003). Furthermore, a desaturase/hydroxylase bifunctional enzyme from *Lesquerella fendleri* has been identified to produce lesquerolic acid (Broun et al., 1998; Moon et al., 2001).

MEDIATORS ON TAG SYNTHESIS AND ACCUMULATION IN WOODY OIL PLANTS

The main lipids store in plants are TAGs. Generalized pathways of TAG synthesis and key mediators on its accumulation especially in the woody oil plants are depicted in this section. Our current investigation on tung tree is also mentioned here.

Pathways leading to TAG formation

Formation of TAG can be achieved in several ways, as shown in Figure 1. The first classical Kennedy pathway (Kennedy, 1961), using acyl-CoA as donor and diacylglycerol (DAG) as acceptor, is catalyzed by enzyme acyl-CoA: diacylglycerol acyltransferase (DGAT) and transfers an acyl group from acyl-CoA to sn-3 of DAG and forms TAG. The second is acyl-CoA independent pathway, which uses phosphatidylcholine (PC) as acyl donors and DAG as acceptor, catalyzed by an enzyme called phospholipids: diacylglycerol acyltransferase (PDAT), which can transfer the sn-2 acyl chain from PC to DAG, forming lyso-PC and TAG (Dahlqvist et al. 2000). Also the acyl-CoA independent pathway can be catalyzed by DGAT, using two molecules of DAG to produce TAG and monoacylglycerol (MAG) (Weselake, 2005).

Key mediators involved in TAG biosynthesis and manipulation

Much more attention has been focused on the enzymes involved in the TAG synthesis: phospholipase A_2 (PLA2) and G-3-P acyltransferase (GPAT), as well as phospholipids: diacylglycerol acyltransferase (PDAT), Lyso PA acyltransferase (LPAAT) and diacylglycerol acyltransferase (DGAT). Currently, at least eight GPAT genes have been identified in *Arabidopsis thaliana*, but neither of them has been shown important in seed TAG biosynthesis (Beisson et al., 2007). PDAT catalyses the acyl transfer from PC to SN-1,2-DAG to yield TAG. But little evidence has been found to date that it plays a major quantitative or qualitative role in seed TAG metabolism (Dahlqvist et al., 2000). LPAAT genes have been proven to be useful for increasing the accumulation of target fatty acids in TAG in transgenic crops. Scarce information of these genes in woody plant has been obtained. Considering the development of woody oil plants seeds metabolic engineering, knowledge-based gene discovery and application are urgently required.

Now there is general agreement that diacylglycerol acyltransferases (DGATs) exert a strong influence on the amount and composition of TAG synthesized in developing seeds. DGAT catalyzed the committed step of oil biosynthesis by transferring a fatty acyl group from acyl-CoA to a diacylglycerol substrate to form TAG (Figure 1), and can also could employ two molecules of DAG to produce TAG and monoacylglycerol (MAG). At least three different and structurally unrelated enzymes catalyze DGAT activity, including DGAT1, DGAT2 (Shockey et al., 2006) and DGAT3 (Saha et al. 2006). For woody oil plants, DGAT1 and DGAT2 have been investigated in Tung tree, where DGAT2 is strongly induced in developing seeds, and the timing of DGAT2 gene expression coincides closely with the onset of eleostearic acid biosynthesis and total oil accumulation. Expression of tung tree DGAT2 in yeast cells resulted in elevated accumulation of TAG than DGAT1 (Shockey et al., 2006). Currently, it has been reported that DGAT1-2 with F469 a phenylalanine insertion is responsible for the increased oil and fatty acid contents in maize (Zheng et al., 2008). Lardizabal et al. (2008) showed that expression of a codon-optimized version of DGAT2A from soil fungal *Umbelopsis ramanniana* in soybean resulted in oil increase in seeds (Lardizabal et al., 2008), which offered an original indication for DGAT transgenic engineering. In addition to catalyzing a critical role in TAG synthesis,

Table 1. Woody oil plants resources summarization and their oil amounts.

Woody plant species	Oil position	Oil (%)	Woody plant species	Oil position	Oil (%)
Aconitum flavum	seed	46.9	*Lasiococca comberi*	seed	59.3
Actinodaphne obovata	kernel	51	*Lindera aggregata*	seed	53.1
Aleurites moluccana	kernel	65.4	*Lindera caudata*	Fruit	50.5
Amesiodendron chinense	kernel	50.9	*Lindera chienii*	seed	49.3
Anacardium occidentale	kernel	50.1	*Lindera chunii*	seed	54.1
Arachis hypogaea	kernel	50.7	*Lindera communis*	seed	53.1
Butyrospermum parkii	kernel	52.5	*Lindera latifolia*	seed	57.6
Carya cathayensis	kernel	67.1	*Lindera megaphylla*	seed	52.2
Carya hunanensis	kernel	54.8	*Lindera metcalfiana*	seed	57.3
Carya illinoensis	kernel	63.5	*Lindera nacusua*	kernel	61.6
Camellia furfuracea	kernel	52.1	*Lindera reflexa*	seed	52.5
Camellia microphylla	kernel	59.2	*Lindera thomsonii*	seed	50.5
Camellia obtusifolia	kernel	50.5	*Litsea chunii*	seed	49.4
Camellia oleifera	kernel	49.4	*Litsea coreana*	seed	61.9
Camellia pitardii	kernel	56	*Litsea cubeba*	seed	49.1
Camellia reticulata	kernel	58.3	*Litsea elongata*	seed	53
Camellia sasanqua	kernel	47.6	*Litsea euosma*	kernel	56.2
Camellia semiserrata	kernel	63	*Litsea glutinosa*	kernel	57.5
Camellia vietnamensis	kernel	48.1	*Litsea panamonja*	kernel	51.2
Canarium album	kernel	58.1	*Litsea populifolia*	Fruit	49.4
Canarium bengalense	kernel	57	*Litsea pungens*	kernel	55.4
Canarium pimela	kernel	59.4	*Litsea rotundifolia*	seed	62.5
Celtis wightii	kernel	68.1	*Macaranga adenantha*	kernel	60.3
Cephalotaxus fortunei	kernel	63.6	*Macadamia ternifolia*	kernel	66.5
Cephalotaxus sinensis	kernel	63.3	*Madhuca pasquieri*	kernel	46.6
Cerbera manghas	kernel	59.1	*Malania oleifera*	kernel	58.2
Cinnamomum burmannii	seed	59.4	*Maytenus austroyunnanensis*	seed	57.4
Cinnamomum glanduliferum	kernel	59.9	*Maytenus hookeri*	seed	56.6
Cinnamomum japonicum	seed	58.3	*Mesua nagassarium*	kernel	76.5
Cinnamomum porrectum	kernel	55.4	*Melliodendron xylocarpum*	kernel	49.6
Cinnamomum saxatile	kernel	54.8	*Momordica macrophylla*	kernel	46.4
Cinnamomum septentrionale	kernel	56.3	*Neocinnamomum caudatum*	kernel	57.4
Citrus grandis	kernel	49.5	*Neocinnamomum delavayi*	kernel	62.8
Citrus reticulata	kernel	46.8	*Neolitsea aurata*	seed	54.1
Cocos nucifera	fruit	59.3	*Neolitse phanerophlebia*	Fruit	51.4
Cordia dichotoma	seed	51.8	*Neolitsea umbrosa*	Fruit	57.5
Corylopsis multiflora	kernel	51.5	*Ostodes paniculatus*	kernel	55
Corylus ferox	fruit	62.9	*Persea americana*	fruit	50
Corylus heterophylla	fruit	54.4	*Pinus armandi*	kernel	57.1
Corylus mandshurica	fruit	63.8	*Pinus koraiensis*	kernel	69.7
Delavaya yunnanensis	kernel	70	*Pistacia chinensis*	Fruit	24.4
Deutzianthus tonkinensis	kernel	49.7	*Polyalthia plagioneura*	kernel	54.7
Diplopanax stachyanthus	kernel	57.1	*Podocarpus nagi*	kernel	48.4
Dracontomelon duperreanum	kernel	64	*Prunus amygdalus*	kernel	58.4
Dracontomelon macrocarpum	kernel	69.5	*Prunus armeniaca*	kernel	51.9
Dysoxylum binectariferum	Fruit	52.2	*Prunus davidiana*	kernel	50.9
Eberhardtia aurata	kernel	51.3	*Prunus mira*	kernel	50.6
Eberhardtia tonkinensis	kernel	57.5	*Prunus sibirica*	kernel	49.9
Elaeis guineensis	fruit	65.6	*Prunus undulata*	kernel	54.2
Euonymus acanthocarpus	seed	47	*Pterospermum menglungense*	seed	47.6

Table 1. Contd.

Euonymus carnosus	seed	47.8	*Pyrularia edulis*	kernel	62.5
Euonymus grandiflorus	seed	51.2	*Pyrularia sinensis*	kernel	60.7
Euonymus hamiltonianus	seed	52.6	*Sarcandra glabra*	seed	51.2
Euonymus laxiflorus	seed	46.3	*Santalum album*	kernel	62.6
Euonymus macropterus	seed	47.5	*Sapium japonicum*	seed	54.7
Euonymus myrianthus	seed	49.3	*Schleichera trijuga*	kernel	68.8
Euonymus streptopterus	seed	47.4	*Scleropyrum wallichianum*	kernel	66.4
Fagus longipetiolata	seed	42.8	*Sesamum indicum*	seed	51.1
Handeliodendron bodinieri	kernel	52.6	*Sloanea hemsleyana*	seed	51
Hodgsonia macrocarpa	kernel	64.2	*Sloanea sinensis*	seed	49.5
Horsfieldia pandurifolia	kernel	56.2	*Styrax confusus*	kernel	52.8
Hydnocarpus	kernel	51.2	*Sumbaviopsis albicans*	kernel	58.2
Juglans cathayensis	kernel	68.6	*Thevetia peruviana*	kernel	72.4
Juglans mandshurica	kernel	68.2	*Treminalia catappa*	kernel	59.4
Juglans regia	kernel	66.2	*Trewia nudiflora*	kernel	57.9
Juglans sigillata	kernel	69.4	*Tutcheria championi*	kernel	59.1
Jatropha curcas	kernel	56.6	*Tutcheria hirta*	kernel	64.9
Keteleeria davidiana	seed	47.9	*Vernicia montana*	kernel	52.5
Keteleeria evelyniana	seed	59.7	*Vernicia fordii*	kernel	80.0
Keteleeria fortunei	seed	48.4	*Xanthoceras sorbifolia*	kernel	59.9

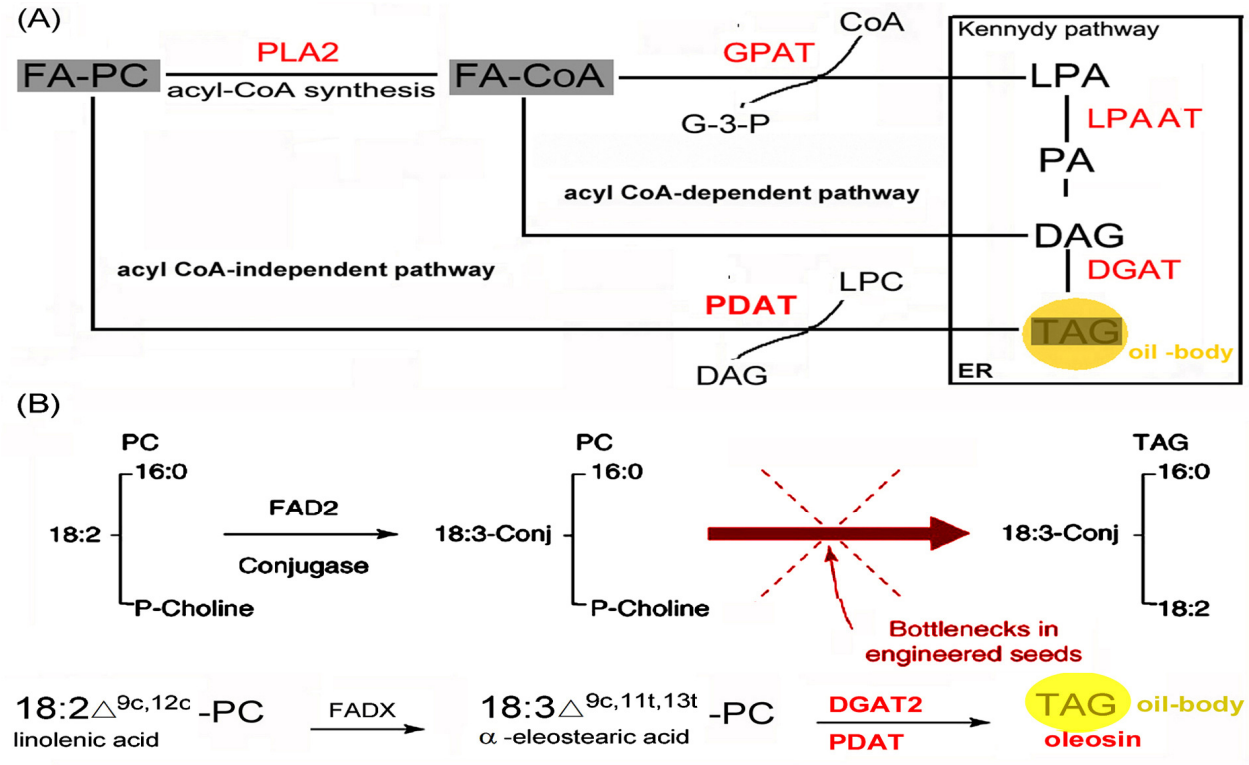

Figure 1. (A) The general pathway of TAG synthesis and accumulation. The first is classical Kennedy pathway catalyzed by enzyme GPAT, LPAAT and DGAT. The second is acyl-CoA independent pathway catalyzed by enzyme PDAT. The fatty acids flux between FA-PC, FA-CoA and TAG determine the final TAG level. (B) The bottlenecks in engineering plants to accumulate TAG enriched novel fatty acids are the low production of TAG but high FA-PC.

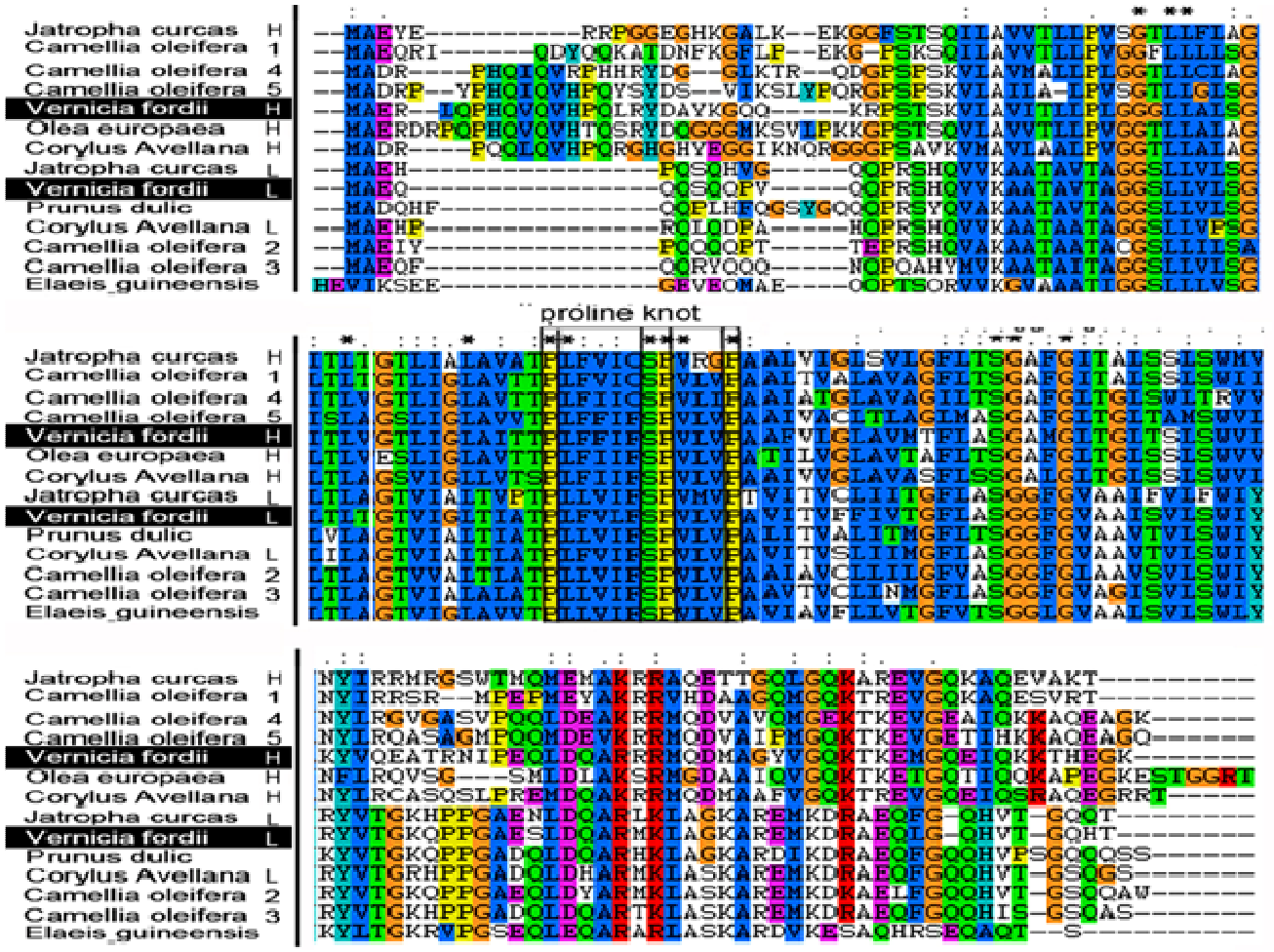

Figure 2. The homology of oleosins in woody plants. There is conserved "proline knot": PX_5SPX_3P-. The oleosin of *V. fordii* is mostly homologous to *Jatropha curcas* and *C. oleifera*.

DGAT also has been shown involved in lipid metabolism associated with germination and leaf senescence. Furthermore, DAGT2 has been reported as a key regulator on solving the "bottleneck" (Figure 1), that is, the low TAG production in transgenic plants (Cahoon et al., 2007). In a word, the work above highlights DGATs as promising targets for manipulating TAG content and the constituent fatty acids.

Oleosins - the proteins could modulate oil body structure and TAG accumulation

TAGs accumulate in structures known as oil bodies or oleosomes, the number and size of which are correlative with TAG content. Oil bodies vary in diameter from about 0.6 to 2 μm (Huang, 1992) and comprise a matrix of TAG surrounding by a phospholipids monolayer embedded by one major type of proteins called oleosins, which are usually presented as two or more isoforms and mainly expressed in seeds. Oelosins share similar structure properties including a long hydrophobic domain around a 12-amino acid motif called a proline knot (Abell et al., 1997), both of which are essential for correct targeting to oil bodies (Van Rooijen and Moloney, 1995). Oleosins promote steric hindrance and electrical repulsion between oil bodies and prevent the organelles from coalescing during seed maturation, desiccation and germination (Tzen et al., 1992; Leprince et al., 1998). Oleosins accumulation has been proved to determine the size of oil bodies through the experiment that oleosin suppression resulted in an aberrant phenotype of embryo cells that contain unusually large oil bodies (Siloto et al., 2006). We first isolated oleosin cDNAs from *V. fordii*; they are most homologous to those in *J. curcas* and *C. oleifera* in oil woody plants, as indicated in Figure 2.

Moreover, the suppression of oleosins had a small but statistically significant effect on fatty acid preferences in TAG (Siloto et al., 2006). Therefore, the introduction of a foreign oleosin may be an alternative way to choose fatty acid and increase TAG accumulation through modulating oil body size.

Direction of fatty acids flux into TAG

The production of high TAG level enriched novel fatty acid is the pursuit of biologists. But most of the cases are undesirable especially in transgenic plants. The exotic fatty acids generally could not be stored in the right place. Most of them are integrated in phosphatidylcholine (PC) instead of storing in oil bodies and ultimately in TAG form, depicted as Figure 1B. For example, FAD2-like genes isolated from *Morordica charantia* and *Impatiens balsamina* produce α–eleostearic acid and α–parinaric acid in transgenic plants only at a third of the level in the native species (Cahoon et al., 1999). The results strongly indicated that there is a fatty acid channel into TAG after synthesis. The direction of fatty acids flux between the PC, acyl-CoA and TAG pools determines final TAG level (Lardizabal et al., 2008) (Figure 1A). The above key mediators in TAG synthesis, including GPAT, LPAAT, DGAT and PDAT, seemed to be involved in prevention of the unusual fatty acids in PC and other membrane phospholipids and directs them into TAG. Among them, DGATs enzymes are proven to be more crucial for the direction of fatty acid flux into TAG (Zheng et al., 2008; Shockey et al., 2006; Kroon et al., 2006).

CONCLUSION AND PERSPECTIVES

Woody oil plants, as a substitute of oil crops to supply petroleum-derived materials and wide application in industry, have a prominent future. However, large-scale production of these woody oil plant species through traditional farming and breeding procedure has a diversity of problems, such as poor agronomic traits and management. With the fast development of molecular biology and the study on the model plants, the most promising route to the development of such renewable resources is via oilseed genetic engineering. Recently, knowledge about TAG synthesis and accumulation in woody oil plants has been gradually realized. Tung tree for example, FAD2, FAX, Oleosins, DGAT1 and DGAT2 has been well studied, but for the woody oil plants, there is still a long way to go to obtain useful information.

In view of complicated processes participating in TAG synthesis and accumulation, the three aspects should be taken into account in increasing TAG accumulation. The first is that the multi-play and multi-level regulation should be elucidated. In transgenic plants, the mediators always cooperate at transcriptional and translational level. The second is the cellular regulation of mediators. The compartmentalization of enzymes activity within specific regions or subdomains of the ER might be essential for both novel fatty acid synthesis and their channeling into TAG (Dyer and Mullen, 2008). The biochemical and immunolocalization studies of FAD2-like enzyme, such as fad2 and FADX in tung tree, have shown their location exclusively in the ER and this introduces a sort of topological orientation in ER membranes (Dyer et al. 2002). DGATs are also localized in subdomains of ER and hold potential for compartmentalization of oil biosynthesis (Shockey et al., 2006; Dyer and Mullen, 2008). The third aspect is that the environmental factors including light intensity, temperature, mineral deprivation, osmotic agent, together with alteration of carbon source also contribute to the process of TAG accumulation and so should be considered in farming and management.

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