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Genes Involved in Lipid Metabolism in Coconut

Wei Xia

Abstract

Coconut palm (*Cocos nucifera* L) is an economically important monocot plant grown in tropical and subtropical regions. Coconut oil is stored in a solid endosperm and has 47.48–50.5% fatty acid component as lauric acid (C12:0). Present research showed that acyl-acyl carrier protein thioesterases (FatA/B) and lysophosphatidic acid acyltransferase (LAAPT) are key enzymes determining medium-chain fatty acid accumulation in coconut oil. Among five *CnFatB* genes, *CnFatB3* expressed specifically in endosperm and *in vitro* experiment showed that this gene made mainly lauric acid (C12:0) and tetradecenoic acid (C14:1). Overexpression of *CnFatB3* in *Arabidopsis* increased the amounts of C12:0 and C14:0 in transgenic plant. *CnLPAAT* gene that is expressed specifically in coconut endosperm showed a preference for using acyl-CoAs containing C10:0, C12:0, and C14:0 acyl groups as acyl-donor substrates. Coconut and oil palm are closely related species with approximately 50% lauric acid (C12:0) in their endosperm. The two species have a close evolutionary relationship between predominant gene isoforms and high conservation of gene expression bias in the lipid metabolism pathways. Moreover, since no stable transformation system has been constructed in coconut palm, gene function validations have been done *in vitro*, or genes transformed into a heterologous system.

Keywords: medium-chain fatty acid, lipid metabolism, coconut endosperm, gene evolution, de novo fatty acid synthesis, TAG biosynthesis

1. Introduction

Coconut palm (*Cocos nucifera* L), belonging to the Arecaceae family, is an economically important monocot plant grown in tropical and subtropical regions. Coconut kernels have approximately 63.1% oil content in a solid endosperm (copra) [1]. A noticeable feature of coconut oil is that 47.48–50.5% of its fatty acid component is lauric acid (C12:0), which is a type of medium-chain fatty acid (MCFA) [2]. A closely related species of coconut, the African oil palm, also contains 50% lauric acid in its kernel oil [3]. The lauric acid content of coconut oil makes it useful for a range of edible and nonedible purposes. A number of genes differentially expressed in coconut endosperm have been identified by suppression subtractive hybridization [4]. *Arabidopsis* has more than 600 genes involved acyl-lipid metabolism, and Xiao et al. [5] identified 806 orthologous genes of these *Arabidopsis* genes in coconut palm based on the first version of coconut genome sequences [1, 2]. A better understanding of lipid biosynthesis and tissue-specific transcription could help breeding efforts to improve the content and composition of coconut oil used

Coconut gene ID	Protein	Annotation	Gene validated in reference
CCG009120.1	PDH-E1 α	E1-alpha component of pyruvate dehydrogenase complex	
CCG003104.1	PDH-E1 β	E1-beta component of pyruvate dehydrogenase complex	
CCG004328.1,CCG016344.1,CCG020484.1,CCG022353.1	LTA1	Dihydrolipoamide acetyltransferase, E2 component of pyruvate dehydrogenase complex	
CCG022878.1	LTA2	Dihydrolipoamide acetyltransferase, E2 component of pyruvate dehydrogenase complex	
CCG016999.1	LPD2	Dihydrolipoamide dehydrogenase, E3 component of pyruvate dehydrogenase complex	
CCG004885.1	CT- α	Carboxyltransferase-alpha; subunit of heteromeric ACCase	
CCG016556.1	BCCP	Biotin carboxyl carrier protein of heteromeric ACCase	
CCG014874.2,CCG016422.1	BC	Biotin carboxylase of heteromeric ACCase	
CCG000475.1,CCG019561.1	MCMT	Malonyl-CoA: ACP malonyltransferase	
CCG001191.1,CCG001193.1,CCG001194.1,CCG024029.1,CCG026381.1	KASI	Ketoacyl-ACP Synthase I	[6]
CCG000907.1,CCG015780.2,CCG023608.3	KASII	Ketoacyl-ACP Synthase II	
CCG003289.1,CCG025932.1	KASIII	Ketoacyl-ACP Synthase III	
CCG006105.2,CCG025988.1,CCG014527.1,CCG024266.1	KAR	Ketoacyl-ACP Reductase	
CCG007292.1,CCG001741.1	HAD	Hydroxyacyl-ACP Dehydratase	
CCG019022.2,CCG019145.2	ENR1	Enoyl-ACP Reductase	
CCG001923.1	ACP1	Acyl carrier protein	
CCG000806.1,CCG000980.1,CCG017093.1,CCG026999.1,CCG027016.1,CCG027238.1	ACP4		

Coconut gene ID	Protein	Annotation	Gene validated in reference
CCG025689.1	DES6	Stearoyl-ACP desaturase	[7]
CCG005175.1,CCG011462.1,CCG019622.1	FAB2		
CCG017191.1,CCG017192.1,CCG017193.1,CCG021345.1	DES5		
CCG005178.1,CCG012754.1	FatA	Acyl-ACP thioesterase A	[8, 9]
CCG006479.1,CCG007799.1,CCG011598.1,CCG015192.1,CCG019705.1	FATB	Acyl-ACP thioesterase B	
CCG005500.1	HACPS	Holo-ACP synthase	
CCG001744.2,CCG007290.1,CCG007291.1	LACS9	Long-chain Acyl-CoA synthetase	

Table 1.
Coconut genes belong to de novo fatty acid biosynthesis.

Coconut gene ID	Protein	Annotation	Gene validated in reference
CCG004869.3,CCG020141.3,CCG023968.1,CCG027042.1	GPDH	NAD-dependent glycerol-3-phosphate dehydrogenase	
CCG019614.2	GPAT9	Glycerol-3-Phosphate acyltransferase (mammalian homolog)	
CCG006531.1,CCG015599.1,CCG016821.1	LPAAT2	1-Acylglycerol-3-phosphate acyltransferase	[6, 10–13]
CCG022695.1	PAH1	Phosphatidate phosphatase	
CCG009829.1,CCG016247.2	PAH2	Phosphatidate phosphatase	
CCG007725.1,CCG026806.1	LPP- β	Phosphatidate phosphatase	
CCG003641.1,CCG010800.1	LPP- δ	Long chain base 1-phosphate phosphatase	
CCG015429.1,CCG019248.1	DGAT1	Acyl-CoA:diacylglycerol acyltransferase	
CCG004186.1,CCG026159.1	DGAT2	Acyl-CoA:diacylglycerol acyltransferase	[14]
CCG015380.1	DAcT	Wax synthase-like	
CCG005217.1	PDAT1	Phospholipid:diacylglycerol acyltransferase	
CCG019998.1,CCG019999.1,CCG020055.1	PDAT-related?	Phospholipid:acyl acceptor acyltransferase	
CCG011285.1,CCG021291.1	LPEAT1	1-Acylglycerol-3-phosphoethanolamine acyltransferase	
CCG000909.1,CCG000910.1	LPEAT2		
CCG002335.2,CCG015142.3	LPCAT	1-Acylglycerol-3-phosphocholine acyltransferase	
CCG017936.1	PDCT/ROD1	Phosphatidylcholine:diacylglycerol cholinephosphotransferase	
CCG019021.1,CCG019148.1	FAD2	Oleate desaturase	
CCG003640.4,CCG010801.1	CDP-DAGS	CDP-DAG synthase	
CCG021791.1	DAG-CPT	Diacylglycerol cholinephosphotransferase	
CCG009590.1,CCG024101.3,CCG025115.1	CK	Choline kinase	
CCG007754.1,CCG019356.1,CCG026050.3	CCT2	Choline-phosphate cytidyltransferase	

Coconut gene ID	Protein	Annotation	Gene validated in reference
CCG021844.1	ACBP2	Acyl CoA binding protein	
CCG005041.1,CCG008659.2,CCG018700.1	ACBP3		
CCG009417.1,CCG020854.1,CCG026758.2	ACBP4		
CCG000884.2,CCG026958.1	ACBP6		
CCG009767.1,CCG016753.1,CCG016754.2	LACS4	Long-chain Acyl-CoA synthetase	
CCG027986.1,CCG027990.1	NMT1	Phosphoethanolamine N-methyltransferase	
CCG009861.1	PIS2	Phosphatidylinositol synthase	
CCG026466.1	PSD1	Phosphatidylserine decarboxylase	
CCG023785.2	PSD3		
CCG005386.2,CCG012449.1,CCG015191.4	PSS	Base-exchange-type phosphatidylserine synthase	
CCG001187.2,CCG026384.1	EK	Ethanolamine kinase	
CCG000220.1,CCG001400.4,CCG005823.1,CCG026528.2	PECT1	CDP-ethanolamine synthase	

Table 2.
Coconut genes involved in TAG biosynthesis.

for food and other applications. The most noticeable feature of coconut oil is that the major components of fatty acids are medium-chain fatty acid. This feature has attracted the attention of researchers and become the focus of coconut oil research. What genes related with the accumulation of medium-chain fatty acid in endosperm? How these genes were evolved and related to a closely related species—oil palm (*Elaeis guineensis*), which also has MCFA as its main fatty acid component in endosperm?

We had reviewed three parts of research related to coconut lipid metabolism in this chapter. Firstly, we summarized key genes related to MCFA accumulation in coconut endosperm. Secondly, we summarized the evolutionary relationship between coconut palm and oil palm for MCFA accumulation. Thirdly, we include descriptions of in vivo and in vitro gene validation experiments. Two tables provide coconut genes related to de novo fatty acid biosynthesis (**Table 1**) and triacylglycerols (TAG) biosynthesis (**Table 2**).

2. Genes related to lipid metabolism in coconut palm

Coconut palm stores oil in endosperm tissues, and its fatty acid composition changes in different developing stages of endosperm [4, 5]. The proportion of lauric acid increases with the maturing process of coconut fruit and reaches the peak when the fruit matures. The comparison of gene expression for different developing stages of endosperm indicated that the expression levels of stearoyl-acyl carrier protein desaturase, acyl-ACP thioesterase B (FatB), and lysophosphatidic acid acyltransferase (LPAAT) arose along with the endosperm development [4]. Xiao et al. [5] identified 71 genes belonging to plastidial fatty acid synthesis pathway in coconut, and 62 enzymes catalyze the conversion of pyruvate to fatty acid (**Table 1**). Moreover, the 17 plastidial proteins involved in the conversion of pyruvate to fatty acids were five- to sixfold higher in the endosperm than in the leaf or embryo tissue, such as acyl carrier protein (ACP), ketoacyl-ACP reductase (KAR), hydroxyacyl-ACP dehydratase (HAD), and pyruvate dehydrogenase complex (PDHC). TAG is a compact molecule for energy and carbon storage in organisms. Thus, another key pathway for oil storage—triglycerides (TAG) synthesis is analyzed for coconut palm and 69 genes were identified (**Table 2**). Key genes in the two pathways were deeply analyzed through in vivo and in vitro assays, including FatB, LPAAT, and orthologs of *Arabidopsis* *WRINKLED 1* (*WRI 1*) [9, 11, 14, 15].

2.1 Genes related to MCFA accumulation in coconut endosperm

2.1.1 Acyl-acyl carrier protein thioesterases

Acyl-acyl carrier protein thioesterases (acyl-ACP TEs) terminate acyl chain elongation during de novo fatty acid biosynthesis. This reaction is the biochemical determinant of the fatty acid compositions of storage lipids. There are two classes of acyl-ACP TEs—FatA and FatB. Since 1996, researchers have cloned acyl-ACP TEs from California bay laurel (*Umbellularia californica*) and validated its role in accumulating MCFA by transforming it into rapeseed (*Brassica napus*). Further research has classified FatB genes into three classes based on their specificities: class I acyl-ACP TEs act primarily on 14- and 16-carbon acyl-ACP substrates; class II acyl-ACP TEs have broad substrate specificities, with major activities toward 8- and 14-carbon acyl-ACP substrates; and class III acyl-ACP TEs act predominantly on 8-carbon acyl-ACPs.

Coconut palm has two acyl-ACP thioesterase A (FatA) genes in coconut palm and five FatB genes, which were CnFatB1 (CCG011598.1), CnFatB2-1 (CCG006479.1), CnFatB2-2 (CCG007799.1), CnFatB3 (CCG019705.1), and CnFatB4 (CCG015192.1). Three FatB genes were highly expressed in more than one analyzed tissue: CnFatB2-1 (leaf and embryo), CnFatB2-2 (leaf, embryo, and endosperm), and CnFatB3 (embryo and endosperm). Three acyl-ACP TEs of coconut (CnFatB1, CnFatB2, and CnFatB3) indicated divergent specificity: CnFatB1 (JF338903) and CnFatB2 (JF338904) produced major fatty acids as myristic acid (C14:0) and palmitoleic acid (C16:1); CnFatB3 (JF338905) made mainly lauric acid (C12:0) and tetradecenoic acid (C14:1) [14]. Yuan et al. transformed and overexpressed CnFatB3 in *Arabidopsis*, and the transgenic plants increased the amounts of 12:0 (lauric acid), 14:0 (myristic acid), 16:0 (palmitic acid), and 18:0 (stearic acid) by 30-, 80-, 4-, and 2-fold, respectively [6].

2.1.2 Lysophosphatidic acid acyltransferase

Coconut oil has 92% saturates and most of its TAGs are trisaturated. Moreover, laurate is found enriched at sn-2 position, which is catalyzed by membrane-bound lysophosphatidic acid acyltransferase (LPAAT) enzyme. Davies et al. detected an enzyme from coconut endosperm, which is a laurate-CoA-preferring LPAAT and active during endosperm maturation [9]. The LPAAT enzyme prefers acyl-CoAs containing C10:0, C12:0, and C14:0 acyl groups as acyl-donor substrates [9]. Knutzon et al. [11] performed the LPAAT protein purification and cloned the corresponding cDNA of this gene from coconut. The gene was then transformed and expressed in *Escherichia coli*, and substrate activity profile of this gene matched that of the coconut enzyme. This copy of LPAAT is the gene named as CCG001603.1 in the first version of coconut genome sequence [5]. Knutzon et al. transformed this gene into a rapeseed transgenic gene line which is expressed of a California bay laurel (*Umbellularia californica*) 12:0-acyl carrier protein thioesterase (BET) and contained up to 50% laurate in its developing seeds [11]. In this transgenic rapeseed with BTE, laurate is found almost exclusively at the sn-1 and sn-3 positions of the triacylglycerols. Coexpression of the coconut *LPAAT* gene in the transgenic rapeseeds facilitates efficient laurate deposition at the sn-2 position and caused the accumulation of trilaurin [11].

Xu et al. cloned the promoter sequence of the LPAAT gene and characterized the promoter by constructing a series of plasmids with promoter sequences with varied length of deletions to promote a β -glucuronidase (GUS) gene. The plasmids were transformed into rice, and the transgenic plants showed that reporter genes with these promoter fragments tend to express specifically in rice endosperm [12]. Yuan et al. transformed *CnLPAAT* into yeast, and tested fatty acid composition indicated that the gene increased the levels of C12:0 and C14:0 in a CnLPAAT-pYES2 transformant [16]. However, heterologous overexpression of CnLPAAT in tobacco (*Nicotiana tabacum* L.) decreased the contents of C12:0 and C14:0 in transgenic tobacco seeds, which could result from low contents of short- and medium-chain FAs (0.22%), which are available in tobacco seeds of the total FAs.

2.1.3 Diacylglycerol acyltransferase

Besides genes important for MCFA accumulation, there are key genes in TAG biosynthesis pathway that influence oil contents and FA composition. Diacylglycerol acyltransferases (DGAT) and phospholipid:diacylglycerol acyltransferases (PDAT) catalyze diacylglycerol (DAG) to form TAG as the final step in TAG synthesis, using either acyl-CoAs or phospholipids. DAG is an important branch

point between storage and membrane lipid synthesis. Coconut palm has three orthologs of AT2G19450 (*AtDGAT1*) and two orthologs of AT3G51520 (*AtDGAT2*). Coconut *DGATs* genes had higher expression level in coconut endosperm than in the leaf and embryo, especially for *DGAT1* isoform CCG007098.3 and *DGAT2* isoform CCG026159.1 [5].

Zheng et al. cloned a *DGAT2* gene from coconut pulp and transferred the gene into the deficient yeast H1246 and *Arabidopsis* [13]. The *DGAT2* gene that is expressed in the deficient yeast had *DGAT* catalysis activity and restored TAG synthesis in the yeast. Further lipid composition analysis showed that *CnDGAT2* has a substrate preference for two UFAs (C16:1 and C18:1) in yeast and linoleic acid (C18:2) in transgenic plants. These results provide knowledge on *CnDGAT2* and offer new insights into TAG assembly in coconut.

2.2 Transcription factors regulating fatty acid biosynthesis

WRINKLED1 (*WRI1*, AT3G54320) directly controls the transcriptional activation of the fatty acid biosynthetic pathway in *Arabidopsis* and belongs to the APETALA2-ethylene-responsive element-binding protein (AP2-EREBP) family [17]. The ortholog of *AtWRI1* in oil palm was validated as a key transcription factor associated with lipid synthesis [3]. In coconut, three AT3G54320 orthologs were found—CCG005292.1, CCG012597.1, and CCG019741.1. CCG005292.1 and CCG012597.1 were expressed in the endosperm but had low expression in leaf and endosperm, while CCG019741.1 has no expression in leaf, embryo, or endosperm [5]. The *CnWRI1* gene copy (CCG012597.1) validated its interaction with the promoter sequence of acetyl-CoA carboxylase by yeast one-hybrid system [15]. Overexpression of *CnWRI1* (CCG012597.1) specifically in *Arabidopsis* seed showed an increase of palmitic acid (C16:0) and linolenic acid (C18:3) but a decrease in oleic acid content [15].

3. Evolutionary relationship between coconut palm and oil palm

Coconut and oil palm are important oil trees grown in tropical region and closely related species with approximately 50% lauric acid (C12:0) in their endosperm. There are 806 and 840 lipid-related genes annotated for coconut and oil palm, respectively [13]. The majority of lipid-related genes between coconut and oil palm were homologous genes, while 72.8% (438/601) of genes in coconut palm were located in homologous segments with oil palm. The two species have a close evolutionary relationship between predominant gene isoforms and high conservation of gene expression bias in the lipid metabolism pathways.

Since coconut and oil palm have high lauric acid (C12:0) in their endosperm, key genes responsible for MCFA also shared high homology in gene copy and expression pattern. Both coconut and oil palm have five *FATB* genes, but only three *EgFatB* genes highly expressed in oil palm mesocarp or endosperm and four *CnFatB* genes were highly expressed in endosperm or embryo. Homologous gene pair—*CnFatB3* and *EgFatB3*—were both highly expressed in their endosperms, which were validated as key genes for MCFA biosynthesis [3, 6]. Another key enzyme—LPAAT, three *AtLPAAT1*, or *AtLPAAT2* orthologs were found in each of coconut and oil palm [5]. The *LPAAT1* genes were clustered into class I and class II, and the class I genes of both species had higher expression levels in endosperm tissue. Moreover, the *LPAAT2* genes were also clustered into two classes, and genes in class II had low or no expression.

For the key transcription factor associated with lipid synthesis—*WRI1*, Xiao et al. [5] identified three *WRI1* genes in coconut and six in oil palm and classified

the genes into three groups based on conserved amino acid sequences. The coconut and oil palm *WRI1* genes in the same group indicated the same expression pattern: group I was highly expressed both in the coconut endosperm and the oil palm endosperm/mesocarp; group II or III has very low or no expression.

4. Methods used in validation gene function in coconut palm

Coconut palm has a long life cycle and takes 5–10 years to start reproductive stage. Since that, using gene overexpression or knockout to analyze gene function in its own plant system will take years to observe the traits related to fruits. At present, no stable transformation system has been constructed in coconut palm. The convenient ways to validate gene function in coconut are testing biochemical feature of proteins *in vitro* or transforming gene into a heterologous system, such as *Arabidopsis*, rice, yeast or *Escherichia coli* (*E. coli*).

4.1 Testing enzyme activity in vitro

Lipid metabolism is composed of more than 120 enzymatic reactions. Validation of gene function related to lipid metabolism could be done by testing enzyme activity in vitro. Davies et al. have isolated CnLPAAT protein from immature coconut seeds and tested the LPAAT activity by adding Acyl-CoA and LPA as substrates [10].

Laurate is found enriched in sn-2, which indicates that a laurate-CoA-preferring LPAAT is active during endosperm maturation. Davies et al. were able to detect such an enzyme from this tissue, which allowed Knutzon et al. [11] to perform protein purification and cloning of a cDNA encoding the 299-amino acid CLP protein from coconut. When expressed in *E. coli*, and using 12:0-LPA as an acceptor, this enzyme preferred medium-chain CoAs over 18:1-CoA as acyl donors. This is a direct evidence that in coconut endosperm, not only had the common fatty acid biosynthesis pathway been modified to produce almost entirely saturated medium chains but at least one enzyme of lipid biosynthesis (LPAAT) had been modified.

4.2 Testing enzyme activity in vivo

Gene function validation has been conducted through gene overexpression in heterologous plant systems which have stable gene transformation system, such as *Arabidopsis*, rice, and tobacco. Functional characterization of CnWRI1 was done by gene overexpression in *Arabidopsis* and rice [15]. Overexpression of CnWRI1 in *Arabidopsis* seeds caused fatty acid composition changes but not for oil content, while overexpression of the gene in rice endosperm increased the starch content and decreased the protein contents [15]. For gene function validation of CnLPAAT (CCG001603.1), this gene was overexpressed in a transgenic oilseed (*Brassica napus*) plant, which expressed a 12:0-ACP thioesterase from California bay laurel (*Umbellularia californica*). The transgenic lines that coexpressed a 12:0-ACP thioesterase and CnLPAAT had increase laurate content from 50 mol% to total laurate levels, which suggested that CnLPAAT facilitates efficient laurate deposition at the sn-2 position [11].

Transient transgenic expression system of tobacco is also widely used for gene function analysis. Genes belonging to lipid metabolism were also validated by this system, investigating the possibility of oil production in non-seeds biomass [18].

Escherichia coli (*E. coli*) strains are commonly used in molecular biology, because the introduction of DNA into *E. coli* is convenient. Since lipid metabolism is basic in all living cells, specific *E. coli* strain with gene mutation could be used for analyzing enzyme functions. Knutzon et al. [11] cloned the CnLAAPT gene copy (CCG001603.1) from coconut endosperm and tested enzyme activity by introducing the gene into *E. coli* strain K27 that has a mutation in the *fadD* gene as well as β -oxidation of fatty acids. Overexpression of this CnLAAPT gene copy caused the accumulation of free fatty acids in the growth medium. Enzymic specificity of three acyl-ACP TEs of coconut (CnFatB1, CnFatB2, and CnFatB3) have been tested by transforming and expressing in *E. coli* K27 and analyzing free fatty acids accumulated in the medium [14].

5. Conclusions

Coconut palm (*Cocos nucifera* L) is an economically important monocot plant grown in tropical and subtropical regions. Coconut oil is stored in a solid endosperm and has 47.48–50.5% fatty acid component, which is a medium-chain fatty acid (MCFA) such as lauric acid (C12:0). Present research showed that acyl-acyl carrier protein thioesterases and lysophosphatidic acid acyltransferase are key enzymes determining MCFA accumulation in coconut oil (**Figure 1**). In this chapter, we reviewed three aspects of research related to coconut lipid metabolism. Firstly, we summarized key genes related to MCFA accumulation in coconut endosperm. Secondly, we summarized evolutionary relationship between coconut palm and oil palm for MCFA accumulation. Thirdly, we described studies using in vivo and in vitro gene validation experiments in coconut palm.

Figure 1.
The diagram of key genes involved in medium-chain fatty acid accumulation in coconut endosperm.

Conflict of interest

The authors declare no conflict of interest.

Appendices and nomenclature

ACP	acyl carrier protein
DGAT	diacylglycerol acyltransferases

FA	fatty acid
FATA	acyl-ACP thioesterase A
FATB	acyl-ACP thioesterase B
HAD	hydroxyacyl-ACP dehydratase
LPAAT	lysophosphatidic acid acyltransferase
PDHC	pyruvate dehydrogenase complex
TAG	triacylglycerols
WRI1	WRINKLED1

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