UNIVERSITI PUTRA MALAYSIA

TRANSCRIPTOME ANALYSIS OF MESOCARP TISSUES IN OIL PALM (*Elaeis guineessis* Jacq.) MPOB-ANGOLA DURA ACROSS VARIOUS DEVELOPMENTAL STAGES

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By

PRISCILLA ELIZABETH MORRIS

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in Fulfilment of the Requirements for the Degree of Master of Science

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November 2019

Chairman : Datin Siti Nor Akmar Abdullah, PhD
Institute : Tropical Agriculture and Food Security

Oil palm *(Elaeis guineessis)* Malaysian Palm Oil Board (MPOB) Angolan germplasm materials were evaluated for their potential use in oil palm breeding programmes. Large fruit characteristic of some Angola *dura* palms has provided breeders with a source of favourable traits for introgression into the current planting materials. With the aim of understanding molecular regulation during mesocarp development, maturation and ripening of Angola *dura* palms, efforts were initiated to profile the expression of transcripts across nine different developmental stages of mesocarp tissues. The second objective of this study was to identify differentially expressed genes associated with lipid metabolism, carbohydrate metabolism, transcription factors and plant hormone metabolism in mesocarp. The final objective was to profile the expression of selected WRINKLED1 transcripts across different developmental stages of mesocarp, endosperm and vegetative tissues. A total of 36,675 genes were identified from RNA-Sequencing with 24,226 transcripts successfully annotated with the Plant Reference Sequence Database using BLASTX. Pairwise T-test was performed using TIGR Multiexperiment Viewer and a total of 21,261 transcripts were identified as significantly differentially expressed across all the pairwise comparisons. BLAST2GO analysis assigned 13,996 unigenes with various GO terms. Transcripts associated with lipid metabolic process were highly expressed during lag phase preceding the lipid biosynthesis [(10 to 12 Week After Anthesis (WAA)] and fruit maturation (18 to 20 WAA) stages. Meanwhile, transcripts linked with carbohydrate metabolic process were up regulated during transition of fruit developmental stages from 10 to 12 WAA. Further annotation of the unigenes with KEGG pathway identified 279, 757 and 142

transcripts related to lipid, carbohydrate and hormone metabolisms, respectively. Additionally, plant RefSeq database annotated 272 transcripts encoding transcription factors. The most stable reference genes for RT-qPCR were selected based on RefFinder software. Twenty-seven transcripts from the RNA-Seq data of nine developmental stages associated with lipid, carbohydrate, plant hormone metabolism and transcription factors were chosen for validation of expression levels using Fluidigm 48.48 Real-Time qPCR. Transcripts such as *KAS I, FATA, DGAT, ENR, WRI1* and *bZIP* showed different expression profiles in the MPOB-Angola *dura* as compared to the previously reported data. *WRI1-2* was highly expressed in the mesocarp of MPOB-Angola *dura* at the beginning of oil accumulation from 20 WAA to 24 WAA with $\log_2$ (fpkm) of 4.7, together with the up-regulation of FA (and TAG biosynthetic genes In contrast, *WRI1-4* was highly expressed in the endosperm of MPOB-Angola dura from 8-15 WAA and decreased at 18 WAA with a fold change of 4.9 which corresponded with the expression profiles of *KAS I* in the endosperm tissues. The availability of these transcriptome datasets gives an insight into the transcriptional mechanisms controlling the Angolan *dura* fruit development, maturation and ripening.

Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Master Sains

ANALISIS TRANSKRIPTOM DALAM TISU MESOKARPA KELAPA SAWIT (*Elaeis guineessis* Jacq.) MPOB-ANGOLA DURA MERENTASI PELBAGAI FASA PERKEMBANGAN

Oleh

PRISCILLA ELIZABETH MORRIS

November 2019

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Kelapa sawit (*Elaeis guineessis*) Lembaga Minyak Sawit Malaysia (MPOB) daripada bahan germplasma Angolan telah dinilai untuk kegunaan dalam program pembiakbakaan kelapa sawit. Ciri buah yang besar pada sesetengah palma *dura* Angola telah memberikan sumber ciri-ciri yang menarik untuk para pembiakbaka melakukan introgresi ke dalam bahan penanaman semasa. Dengan tujuan untuk memahami pengawalaturan molekul semasa perkembangan, pematangan dan keranuman mesokarpa palma Angola *dura*, usaha telah dimulakan untuk memprofil pengekspresan transkrip di sembilan peringkat perkembangan tisu mesokarpa yang berbeza. Objektif kedua kajian ini adalah untuk mengenalpasti pengekspresan gen yang berkaitan dengan metabolisme lipid, metabolisme karbohidrat, faktor transkripsi dan metabolisme hormon tumbuhan di dalam mesokarpa. Objektif terakhir adalah untuk memprofil pengekspresan transkrip terpilih WRINKLED1 merentasi pelbagai peringkat perkembangan tisu-tisu mesokarpa, endosperma dan vegetatif. Sejumlah 36,675 gen telah dikenalpasti daripada penjujukan RNA di mana 24,226 transkrip tersebut telah berjaya dianotasikan dengan Pangkalan Data Rujukan Tumbuhan menggunakan BLASTX. Ujian T-test berpasangan dilakukan menggunakan TIGR Multiexperiment Viewer dan sejumlah 21,261 transkrip telah dikenalpasti sebagai transkrip yang diekspres secara signifikan merentasi kesemua perbandingan berpasangan. Analisa BLAST2GO menghasilkan anotasi 13,996 unigen dengan pelbagai istilah GO. Transkrip yang berkaitan dengan proses metabolik lipid telah diekspres secara tinggi semasa fasa lag sebelum biosintesis lipid (10 hingga 12 WAA) dan pada peringkat pematangan buah (18 hingga 20 WAA). Sementara itu, transkrip

yang berkaitan dengan proses metabolik karbohidrat meningkat semasa peralihan peringkat perkembangan buah dari 10 hingga 12 WAA. Seterusnya, anotasi ke atas unigen menggunakan tapakjalan KEGG telah mengenalpasti 279, 757 dan 142 transkrip yang masing-masing berkaitan dengan metabolisme lipid, karbohidrat dan hormon. Tambahan pula, anotasi ke atas unigen menggunakan pangkalan data RefSeq tumbuhan telah menunjukkan bahawa 272 transkrip adalah berkaitan dengan faktor transkripsi. Gen rujukan yang paling stabil untuk RT-qPCR telah dipilih berdasarkan perisian RefFinder dan penilaian komprehensif. Dua puluh tujuh transkrip daripada data penjujukan RNA ke atas sembilan peringkat perkembangan yang berkaitan dengan metabolisme lipid, karbohidrat, hormon tumbuhan dan faktor transkripsi telah dipilih untuk pengesahan tahap pengekspresan menggunakan Fluidigm 48.48 qPCR masa nyata. Transkrip seperti *KAS I, FATA, DGAT, ENR, WRI1* dan *bZIP* menunjukkan profil pengekspresan berbeza di antara MPOB-Angola *dura* jika dibandingkan dengan data yang telah dilaporkan sebelum ini. *WRI1-2* telah diekspres secara tinggi di dalam mesokarpa MPOB-Angola *dura* pada peringkat permulaan pengumpulan minyak iaitu daripada 20 hingga 24 WAA dengan peningkatan $\log_2$(fpkm) sebanyak 4.7, bersamaan dengan peningkatan pengekspresan gen-gen yang berkaitan dengan biosintesis asid lemak dan TAG. Sebaliknya, *WRI1-4* telah diekspres di dalam endosperma MPOB-Angola dura dari 8 hingga 15 WAA dan menurun sebanyak 4.9 perubahan lipatan pada 18 WAA di mana profil pengekspresan tersebut adalah berpadanan dengan *KAS I* dalam tisu endosperma. Ketersediaan dataset transkriptom ini meningkatkan pemahaman terhadap mekanisme transkripsi yang mengawalatur fasa perkembangan, pematangan dan keranuman buah Angola *dura*.

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Declaration by graduate student

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LIST OF ABBREVIATIONS

ABA	abscisic acid
5'UTR	5′ untranslated region
ABI3	ABSCISIC ACID INSENSITIVE3
ABI4	ABSCISIC ACID INSENSITIVE4
ABI5	ABSCISIC ACID INSENSITIVE5
ACC Cta	carboxyltransferase a-subunit of heteromeric ACCase
ACC Ctb	carboxyltransferase b-subunit of heteromeric ACCase
ACCase	acetyl-CoA carboxylase
ACO3	1-aminocyclopropane-1-carboxylate oxidase 3
ACP1	acyl-carrier protein 1
ACS	ATP-citrate synthase
ACS-like genes	Asp aminotransferase-like genes
AP2	APETALA 2
ARF	Auxin Responsive factor
ATP	Adenosine Tri-Phosphate
B3 DBD	B3 domain-containing protein
BAM	Binary Alignment Map
BCCP	biotin carboxyl carrier protien of acetyl coenzyme a carboxylase 1
bp	basepair
C 16:0	palmitic acid
C 18:0	stearic acid
C 18:1	oleic acid
C 18:2	linoleic acid

Cdna	complementary DNA
Ct	Cycle threshold
CTAB	Cetyl trimethylammonium bromide
CV	coefficient of variance
CYP	cyclophilin
DAP	days after pollination
DGAT	acyl-CoA:diacylglycerol acyltransferase
Dntp	deoxyribonucleotide triphosphate
EAR	enoyl-ACP reductase
EDTA	ethylenediaminetetraacetic acid
EF1α	elongation factor 1 alpha
EIF4A	eukaryotic initiation factor 4A
eIF-4α	eukaryotic translation initiation factor 4α
EMSA	Electrophoretic mobility shift assay
ENOp	Enolase
ENR	Enoyl-ACP Reductase
ERF	ethylene response factor
EST	expressed sequence tags
EtOH	ethanol alcohol
Ex	PCR amplification efficiencies
FA	fatty acid
FAB	Fatty acid biosynthesis
FAS	Fatty acid synthase
FAS	fatty acid synthesis
FAT	acyl-acyl carrier protein (ACP) thioesterases

FatB	palmitoyl- acyl carrier protein thioesterase
FFB	fresh fruit bunch
fpkm	fragments per kilobase million
FUS3	FUSCA3
GA	gibberellic acid
GA3OX4	gibberellin 3-beta-dioxygenase 4 and lycopene β-cyclase (LCYB)
GAPDH	3-glyceraldehyde phosphate dehydrogenase
GB	giga byte
GMO	genetically modified organism
GO	gene ontology
GOI	gene of interest
GPT2	glutamic pyruvate transaminase
GRAS	Gibberellin-responsive protein
HAD	hydroxyacyl-ACP dehydrase
HK	Hexokinase
HPLC	High-performance liquid chromatography
IAA	indole-3- acetic acid
IAA GH3.5	indole-3-acetic acid-amido synthetase GH3.5
IFC	integrated fluidic circuit
KAR	ketoacyl-ACP reductase
KAS I	ketoacyl-ACP synthase I
KAS II	ketoacyl- ACP synthetases II
KAS III	ketoacyl-ACP synthase III
KEGG	Kyoto Encyclopedia of Genes and Genomes

LACS	long-chain acyl-CoA synthetase
LACS	long chain fatty acid coenzyme a ligase 4
LEC	LEAFY COTYLEDON
LiCl	lithium chloride
LPAAT	1-acylglycerol-3-phosphate O-acyltransferase
M/F	mesocarp to fruit
MAT	malonyl-CoA:ACP malonyltransferase
MeJA	Methyl jasmonate
MFW	mean fruit weight
min	Minute
Mrna	messenger RNA
MSD	manganese superoxide dismutase
NaCl	sodium chloride
NCED1	9-cis-epoxycarotenoid dioxygenase 1
NF-YB-1	nuclear factor Y, subunit B1
NFYC2	nuclear transcription factor Y subunit C-2
NGS	next generation sequencing
nt	Nucleotide
O/B	oil to bunch
OY	oil yield
PCR	Polymerase Chain Reaction
PDH	E2 component of pyruvate dehydrogenase complex
PDHE1b	pyruvate dehydrogenase e1 component subunit β
PEP	phosphoenolpyruvate
PFK	phosphofructokinase

PK	pyruvate kinase
pp2A	protein phosphatase 2A
PPT1	palmitoyl-protein thioesterase
PSY	phytoene synthase
PVP-40	polyvinylpyrrolidone
RGs	reference genes
RIN	RNA Integrity Number
RNA–Seq	RNA Sequencing
Rrna	ribosomal ribonucleic acid
RT-qPCR	Reverse transcription quantitative real-time PCR
SAD	stearoyl ACP desaturases
SAND	SAND family protein
sec3	exocyst complex component sec3
STDEV	standard deviation
TAGs	Triacylglycerols
TFs	transcription factors
TIP41	Tap42-inter-acting protein of 41 kDa
Tris-HCL	tris (hydroxymethyl) aminomethane hydrochloride
TSS	transcription start site
TUB	Tubulin
UBQ	poly-ubiquitin
WAA	weeks after anthesis
WAP	weeks after pollination
WRI1	WRINKLED1
V/V	Volume/ volume

V/V/V	Volume/volume/ volume
W/V	weight of solute /final volume of solution
ZFP-1	zinc finger protein-1
β-TUB	beta tubulin

CHAPTER 1

INTRODUCTION

African oil palm (*Elaeis guineensis*) is a hyperefficient oil-bearing crop, yet ultimatum for edible oils and biofuels, consolidated with sustainability concerns over diminishing rainforest reserves, has led to intense pressure to improve oil palm yield. Despite the fact that it is originated from Africa, oil palm is extensively cultivated in almost 43 countries in the tropical regions of Southeast Asia, Africa, and South America (Koh and Wilcove, 2008). Indonesia and Malaysia monopolize the global production of palm oil, contributing to around 85% of the palm oil production worldwide (Sime Darby Plantation, 2012; Siregar et al., 2012). It was reported that Malaysian Palm Oil Board (MPOB)-Angola *dura* produced 144-150 kg palm^{-1} year^{-1} mean fresh fruit bunch (FFB), 50% mesocarp to fruit (M/F), 15% oil to bunch (O/B), 23 kg palm^{-1} year^{-1} oil yield (OY) (Kushairi et al., 2003). Angola *dura* palm is well known for its large fruit characteristic with a mean fruit weight (MFW) between 24 to 34 g, apart from exhibiting comparable or more variable fatty acid compositions [palmitic acid (C16:0), stearic acid (C18:0), oleic acid (C18:1) and linoleic acid (C18:2)], iodine value and carotene content compared to the commercial *dura x pisifera* (DxP) materials (Kushairi et al., 2003; Rajanaidu et al., 1991). Noh et al. (2002) also reported that Angolan germplasm has lower (29.8% - 48.6%) content of palmitic acid than commercial DxP materials (41.8% - 46.8%). Therefore, there is a demand in increasing the oil price with lower content of palmitic acid and higher content of oleic acid (Noh et al., 2002). Iodine value for Angolan germplasm ranged between 49.6% - 67.4% which was considered as remarkable as compared to the commercial DxP materials. The most important application of the iodine value is to determine the amount of unsaturation contained in FA. It was also tabulated that the carotene content for Angolan germplasm started from 211 ppm to 2604 ppm, which indicated that the carotene levels in some of the Angolan progenies might be greater than the range of carotene content in *E. guineensis* materials (997 ppm for *dura*, 673 ppm for *tenera* and 428 ppm for *pisifera*) reported in this country (Noh et al., 2002). Due to their favourable variation and heritability for several important oil-related traits, Angolan germplasm can be exploited for the genetic improvement of existing planting materials (Noh et al., 2002).

Advances in next-generation sequencing technologies have resulted in RNA Sequencing (RNA–Seq) being widely used for transcriptome profiling. This approach provides more precise measurement of transcript levels and enables the discovery of gene isoforms as compared to other approaches such as microarray and expressed sequence tags (EST) (Wang et al., 2009). RNA-Seq can also be used to investigate splicing variants, gene isoforms, and single nucleotide polymorphisms and post transcriptional modifications (Lalonde et

al., 2011). Through 454 or Illumina sequencing, comprehensive transcriptome sequences were generated for several oil crops such as sesame (Wei et al., 2011), coconut (Fan et al., 2013), avocado (Kilaru et al., 2015) and oil palm (Tranbarger et al., 2011). These data proved useful for gene discovery and development of molecular markers.

Transcriptome analysis across oil palm mesocarp collected from *dura* palms of different origin was performed previously by Tranbarger et al. (2011), whereby a 454 pyrosequencing-derived transcriptome was assembled for developmental phases preceding and during maturation and ripening. They concentrated on the fatty acid and triacylglycerol assembly pathways and during carotenogenesis as high rates of lipid and carotenoid biosynthesis were detected. Guerin et al. (2016) also detected tight transcriptional coordination of fatty acid biosynthesis (FAS) in the plastid with sugar sensing, plastidial glycolysis, transient starch storage and carbon recapture pathways via coexpression network. Recently, oil palm gene model was updated by detailed classification of the oil palm stearoyl-ACP desaturases (*SAD*) and acyl-acyl carrier protein (ACP) thioesterases (*FAT*) genes (Rosli et al. 2018a). Transcriptome analysis across oil palm has enabled the discovery of various isoforms within the four families of acyl-CoA: diacylglycerol acyltransferase (*DGAT*) genes (Rosli et al. 2018b). Evaluation of the *E. guineensis DGAT* gene expression in different tissues and developmental stages suggests that *DGAT* have distinctive physiological roles. Moreover, it was reported that *DGAT* plays a significant role in developmental processes in reproduction, such as flowering, and in fruit/seed formation, particularly in the mesocarp and endosperm tissues (Rosli et al. 2018b). Identification of differentially expressed genes such as *DGAT, SAD, FatA* and *FatB* which are associated with lipid metabolism would be possible through transcriptome profiling of MPOB-Angola *dura* in mesocarp tissues.

Accumulation of up to 90% of oil in the mesocarp involves coordinated regulation of key FAS genes by WRINKLED1 (*WRI1*) transcription factor. Tranbarger et al. (2011) reported that *WRI1* has been described with a transcript profile combined with those of many FAS genes and high lipid accumulation levels, indicating certain specific regulatory characteristics between seeds and fruits. Although it is now confirmed that *WRI1* regulates oil synthesis in both seed and non-seed tissues (Ma et al., 2013; Singh et al., 2013), the master regulators that control the expression of *WRI1* in the oil palm mesocarp remain unclear. Common regulators in seed tissues such as LEAFY COTYLEDON (*LEC1* and *LEC2*), ABSCISIC ACID INSENSITIVE3 (*ABI3*) and FUSCA3 (*FUS3*) genes were not detected. Bourgis et al. (2011) showed that transcripts representing an ortholog of the *WRI1* transcription factor were 57-fold higher in oil palm relative to date palm and displayed a temporal pattern similar to its target genes. Jin et al. 2017 found that the ectopic expression of

EgWRI1-1 in *Arabidopsis* plants dramatically increased the seed mass and oil content. Their findings showed that *EgWRI1* is the key gene that contributed to the hybrid vigor of lipid biosynthesis trait in hybrid *tenera* fruit form. Apart from *WRI1*, two novel transcription factors (TFs), termed *NF-YB-1* and *ZFP-1*, were also found at the core of the FAS regulatory module in oil palm (Guerin et al., 2016). Through transcriptome profiling, idenfication of differentially expressed genes associated with TFs in MPOB-Angola *dura* mesocarp would be possible.

Genes associated with carbohydrate metabolism was also described by Bourgis et al. (2011). Plastid isoforms of ATP-dependent phosphofructokinase (PFK) and pyruvate kinase (PK) have been shown to be up regulated in oil palm and during ripening stage. Additionally, a hike in glutamic pyruvate transaminase (GPT2) and phosphoenolpyruvate (PEP) transporter palmitoyl-protein thioesterase (PPT1) were also reported. Meanwhile, according to Singh et al. (2013), in oil palm, genes implicated in the oxidation of sucrose and the oxidative pentose phosphate pathway were more heavily composed than date palm. To charge glycolytic pathways, pentose phosphates are reprocessed into glucose 6-phosphate, and imports of these cytosolic metabolites involve different transporters on the plastide envelope. Therefore, the accumulation of 90% oil in the mesocarp was strongly due to the channelling of sugars which is destined for oil synthesis. Identification of differently expressed genes associated with carbohydrate such as PK would be possible with transcriptome profiling in MPOB-Angola *dura* in mesocarp tissues.

In oil palm mesocarp, auxin, gibberellic acid and cytokinin rise during the early phase at 60 days after pollination (DAP) and dwindle during 100–120 DAP. Both ethylene (ABA) hormones reach a peak during fruit maturation to ripening phases at 120–160 DAP (Tranbarger et al., 2011). It was also revealed that 1-aminocyclopropane-1-carboxylate oxidase 3 (EgACO3) transcript increased between 120 and 160 DAP (Tranbarger et al., 2011) as the EgACO expression trend correlates with the rise in ethylene observed between 120 and 160 DAP (Tranbarger et al., 2011). Methyl jasmonate (MeJA) which is a methyl ester of jasmonic acid (JA) plays a role a plant growth regulator whereby it has been reported to play an important role in the plant's response to pathogens and wound (Creelman et al., 1992). Interestingly, MeJA also elevated after oil biosynthesis initiated until ripeness in oil palm and 12-oxophytodienoate reductase 3, lipoxygenase 7, jasmonateinduced protein, and allene oxide synthase 1 and 2 are expressed at a higher level in contrast to other jasmonic acid biosynthesis genes (Teh et al., 2014). Identification of differentially expressed genes associated with plant hormone metabolism would be possible with transcriptome profiling of MPOB-Angola *dura* in mesocarp tissues.

Although several research teams have embarked on the journey to gain further understanding on the molecular regulation during development of *dura* fruit form, the transcriptional changes during oil synthesis in this fruit remain limited and restricted to certain genetic background such as Deli and Deli Dabou origin. At MPOB, MPOB-Angola *dura* is being used by breeders as a mother palm for improvement of the current planting materials. However, research thus far has focused on the application of this population for identification of DNA marker related to height increment (Ong et al., 2018). Till date, no research has been carried out to profile the expression of transcripts across MPOB-Angola *dura* fruits. The availability of higher coverage of transcriptome datasets from nine different developmental stages of mesocarp will be able to provide an insight into the transcriptional mechanisms controlling the *dura* fruit development, maturation and ripening.

The specific objectives of this research are:

I. To examine transcriptome profiling across nine different developmental stages of mesocarp from MPOB-Angola *dura*;
II. To identify differentially expressed genes associated with lipid metabolism, carbohydrate metabolism, transcription factors and plant hormone metabolism in mesocarp;
III. To profile expression of selected WRINKLED1 transcripts across different developmental stages of mesocarp, endosperm and vegetative tissues.

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LIST OF PUBLICATIONS

Journal

Morris, P.E., Chan, P.L., Ooi, L.C.L., Ong, P.W., Kamaruddin, K., Marjuni, M., Amiruddin, M.D., Chan, K.L., Rosli, R., Low, E.T.L., Singh, R., Shaharuddin, N.A., Murphy, D.J., Manafi, M. A.A and Abdullah, S.N.A. (2020). Transcriptome analysis across various mesocarp developmental stages of MPOB-Angola *dura*. Journal of Palm Oil Research. https://doi.org/10.21894/jopr.2020.0034.

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Poster presentation

Priscilla Elizabeth Morris, Leslie Ooi Cheng Li, Ong Pei Wen, Katialisa Kamaruddin, Marhalil Marjuni, Mohd Din Amiruddin, Chan Kuang Lim, Leslie Low Eng Ti, Rajinder Singh, Denis Murphy, Noor Azmi Shaharuddin, Siti Nor Akmar Abdullah & Chan Pek Lan. Identification of Differentially Expressed Transcripts across Nine Mesocarp Developmental Stages of MPOB-Angola *Dura*. 12th Malaysia International Genetic Congress. Hotel Bangi Putrajaya Selangor.

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