UNIVERSITI PUTRA MALAYSIA

MOLECULAR CHARACTERISATION AND EXPRESSION PROFILES OF PHOSPHATE-DEFICIENCY INDUCIBLE PHOSPHATE TRANSPORTER 1 AND PHOSPHATE STARVATION RESPONSE GENE FAMILIES IN Elaeis guineensis Jacq.

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By

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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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March 2020

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Institute : Tropical Agriculture and Food Security

Phosphate transporter 1 (PHT1) proteins are responsible for acquisition of phosphate (Pi) by the plants. The transcription factor involved in the transcriptional regulation of *PHT1* is phosphate starvation response (PHR). Pi uptake by PHT1 needs to across a steep concentration gradient from lower Pi concentration in soil, usually less than 10 µM into high Pi concentration inside the plant cells which are in the range of 5 to 20 mM. Moreover, the oil palm plantation requires high fertilizer input to maintain high productivity. But high fertilizer input may cause water pollution. Besides that, Pi rock, the major source of Pi fertilizer is envisaged to be exhausted in next 40 to 70 years. This will cause catastrophic effect to agriculture industry. The objectives of this study were to perform genome-wide molecular characterization of *PHT1* and *PHR* genes in oil palm and study their expression profiles under different Pi-deficient conditions as well as to determine the specific location of EgPHR2 protein using the subcellular localization technique. Using the PHT1 and PHR coding sequences of *Arabidopsis thaliana* and *Oryza sativa* as the query sequences for BLAST search to find the homologues of *PHT1* and *PHR* genes in oil palm resulted in the identifications of 10 *EgPHT1* and three *EgPHR* genes. All EgPHT1 proteins contain GGDYPLSATIxSE, the signature sequence of PHT1. All EgPHR have MYB binding domain and coiled–coil domain characteristic of PHR at their C-terminal regions and one unique SOG2 domain for EgPHR1. Analysis of 1500 bp of promoter sequences on four selected *EgPHT1* genes using PlantCare and New PLACE databases showed that two of the *EgPHT1* (*EgPHT1;4* and *EgPHT1;7*) contain the PHR binding site (P1BS) motif. In addition, other Pi deficiency responsive motifs including W-box and many E-box motifs were found on *EgPHT1;4*, *EgPHT1;6* and *EgPHT1;7* promoter sequences. The root specific motif, ROOTMOTIFTAPOX1 was also discovered on *EgPHT1;4*, *EgPHT1;6* and *EgPHT1;7*. The oil palm seedlings were grown hydroponically under Pi sufficient (+P; 1.93 mM), low Pi (LP; 0.1 mM) and Pi deficient (-P) conditions. The expression of four of the *EgPHT1* and two of the *EgPHR* was studied by real-time quantitative PCR (qPCR) in the roots and leaves of these

seedlings. All genes showed enhanced expression in roots at -P compared to +P. The expression profile of *EgPHR2* which showed upregulation at LP compared to +P and further increase at -P correlated with *EgPHT1;4* and *EgPHT1;7* that possess P1BS motif in their promoter sequences. EgPHR2, as a potential early transcriptional regulator for Pi starvation was detected to be nuclear localized through subcellular localization experiment, a key characteristic of a transcription factor. This study suggests all four analyzed *EgPHT1* and two *EgPHR* play critical role in responding to Pi deprivation in oil palm. *EgPHT1;4* and *EgPHT1;7* which possess the P1BS motif are potentially upregulated by *EgPHR2* as an early response mechanism against Pi starvation. The result from this study will help to fully map the Pi regulatory mechanism to enhance the Pi acquisition efficiency by oil palm.

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

PENCIRIAN SKALA MOLEKUL DAN PENGEKSPRESIAN PROFIL-PROFIL KEKURANGAN FOSFAT TERARUH KELUARGA-KELUARGA GEN *PENGANKUT FOSFAT 1* DAN *TINDAK BALAS KEKURANGAN FOSFAT* DALAM *Elaeis guineensis* Jacq.

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Pengangkut fosfat 1 (PHT1) adalah protin yang bertanggungjawab dalam pengambilan fosfat (Pi) oleh pokok. Faktor transkripsi yang terlibat dalam mengawal trankripsi PHT1 adalah tindak balas kekurangan fosfat (PHR). Pengambilan Pi oleh PHT1 perlu melalui kecerunan kepekatan yang tinggi iaitu daripada kepekatan Pi yang rendah di dalam tanah yang biasanya kurang dari 10 µM kepada kepekatan Pi yang tinggi di dalam sel-sel pokok dalam linkungan 5 ke 20 mM. Selain itu, ladang kelapa sawit memerlukan input baja yang tinggi untuk menjamin kadar produktiviti yang tinggi. Tetapi input baja yang tinggi berkemungkinan akan menyebabkan pencemaran air. Selain itu juga, batu Pi yang merupakan sumber utama kepada baja Pi dijangka akan habis dalam 40 ke 70 tahun akan datang. Ini akan menyebabkan kesan yang dahsyat kepada industri pertanian. Objektif kajian ini adalah untuk melaksanakan pencirian skala molekul pada genom untuk gen-gen *PHT1* dan *PHR* dalam kelapa sawit dan mengkaji pengekspresian profil-profil mereka di bawah keadaan kekurangan Pi yang berbeza serta untuk mengenal pasti lokasi spesifik protin EgPHR2 dengan menggunakan teknik penyetempatan selular-separa. Dengan menggunakan jujukan kodon PHT1 dan PHR daripada *Arabidopsis thaliana* dan *Oryza sativa* sebagai jujukan rujukan, pencarian gen-gen homolog *PHT1* dan *PHR* di dalam kelapa sawit dilakukan dalam carian BLAST yang mana menemukan 10 gen *EgPHT1* dan tiga gen *EgPHR*. Kesemua protin EgPHT1 mempunyai GGDYPLSATIxSE, iaitu jujukan khas untuk PHT1. Domain mengikat MYB dan domain coiled-coil yang merupakan ciri-ciri bagi PHR turut ditemui dalam kesemua EgPHR pada bahagian C-terminal dan tambahan satu domain SOG2 unik turut ditemui pada EgPHR1. Analisis pangkalan data PlantCare dan New PLACE bagi 1500 bp jujukan promoter untuk empat gen *EgPHT1* yang dipilih menunjukkan dua daripada *EgPHT1* tersebut (*EgPHT1;4* dan *EgPHT1;7*) mengandungi motif bahagian cantuman PHR (P1BS). Selain itu, motif-motif lain yang terlibat dengan kekurangan Pi seperti W-box dan beberapa E-box turut dijumpai pada jujukan promoter *EgPHT1;4*, *EgPHT1;6* dan *EgPHT1;7*. Motif spesifik akar, ROOTMOTIFTAPOX1 turut ditemui pada

EgPHT1;4, *EgPHT1;6* dan *EgPHT1;7.* Anak-anak pokok kelapa sawit dibesarkan secara hidroponik dalam keadaan Pi mencukupi (+P; 1.93 mM), kurang Pi (LP; 0.1 mM) dan kekurangan Pi (-P). Pengekspresian empat daripada *EgPHT1* dan dua daripada *EgPHR* di dalam daun dan akar dilakukan dengan menggunakan PCR kuantitatif masa sebenar (qPCR). Kesemua gen menunjukkan peningkatan ekspresi dalam akar pada -P dibandingkan dengan +P. Profil pengekspresian *EgPHR2* yang mana menunjukkan peningkatan regulasi pada LP dibandingkan dengan +P dan kemudian meningkat lagi pada –P berkolerasi dengan *EgPHT1;4* dan *EgPHT1;7* yang mempunyai motif P1BS dalam jujukan promoter mereka. EgPHR2, yang mempunyai potensi sebagai pengawal transkripsi untuk kekurangan Pi dikesan berlokaliti nuklear melalui eksperimen penyetempatan selular-separa, iaitu suatu ciri utama sebagai faktor transkripsi. Kajian ini mencadangkan kesemua empat *EgPHT1* dan dua *EgPHR* yang dianalisa memainkan peranan penting dalam tindak balas terhadap kekurangan Pi di dalam kelapa sawit. *EgPHT1;4* dan *EgPHT1;7* yang mana mempunyai motif P1BS adalah berpotensi ditingkatkan regulasi oleh *EgPHR2* sebagai mekanisme tindak balas awal melawan kekurangan Pi. Hasil dari kajian ini dapat membantu untuk melengkapkan mekanisme pengawalan Pi supaya pengambilan Pi oleh kelapa sawit menjadi lebih efisien.

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This thesis was submitted to the Senate of Universiti Putra Malaysia and has been accepted as fulfillment of the requirement for the degree of Master of Science. The members of the Supervisory Committee were as follows:

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LIST OF ABBREVIATIONS

°	degree
°C	degrees Celsius
+P	Pi sufficient
-P	Pi deficient
α	alpha
β	beta
2D	two dimensional
Al	aluminium
ABRC	Arabidopsis Biological Resource Center
ADP	adenosine diphosphate
AMP	adenosine monophosphate
ATP	adenosine triphosphate
At	*Arabidopsis thaliana*
As	*Astragalus sinicus*
B	Boron
Bd	*Brachypodium distachyon*
bHLH	basic helix-loop-helix
BLAST	Basic Local Alignment Search Tool
Bn	*Brassica napus*
bp	base pairs
Ca	calcium
Cu	copper
Cl	chlorine
CC	coiled-coil

C. reinhardtii	*Chlamydomonas reinhardtii*
cDNA	complementary deoxyribonucleic acid
Ct	cycle threshold
$CaCl_2$	Calcium chloride
$Ca(NO_3)_2$	Calcium nitrate
$CuSO_4$	Copper(II) sulfate
CaMV	Cauliflower mosaic virus
DEPC	Diethyl Pyrocarbonate
DNA	deoxyribonucleic acid
dNTP	nucleoside triphosphate
DOSM	Department of Statistics Malaysia
E. coli	*Escherichia coli*
E. guineensis	*Elaeis guineensis*
E. oleifera	*Elaeis oleifera*
Eg	*Elaeis guineensis*
EDTA	Ethylene Diamine Tetra Acetic Acid
Fe	iron
Fe-NaEDTA	Ethylenediaminetetraacetic acid ferric sodium salt
FELDA	Federal Land Development Authority
FFB	Fresh Fruit Bunches
GAPDH	Glyceraldehyde-3-phosphate dehydrogenase
Gb	Giga base pairs
GDP	Gross domestic product
GFP	green fluorescent protein
GH500	Golden Hope 500 series
GM	genetically modified

Gm	*Glycine max*
Gv	*Glomus versiforme*
H^+	hydrogen ion (or proton)
$H_2PO_4^-$	dihydrogen phosphate ion
H_2SO_4	Sulfuric acid
H_3BO_3	Boric acid
HKT	High-affinity potassium transporter
HPO_4^{2-}	Hydrogen phosphate
JAKIM	*Jabatan Kemajuan Islam Malaysia*
JTT	Jones-Taylor-Thornton
K	Potassium
KH_2PO_4	Monopotassium phosphate
KNO_3	Potassium nitrate
KOH	Potassium hydroxide
LB	Luria-Bertani
Le	*Lycopersicon esculentum*
LiCl	Lithium chloride
Lj	*Lotus japonicas*
LP	low phosphate
Lu	*Linum usitatissimum*
M	molar
MEGA	Molecular Evolutionary Genetics Analysis
MFS	major facilitator superfamily
Mg	magnesium
$MgSO_4$	Magnesium sulfate
Mn	manganese

$MnSO_4$	Manganese (II) sulfate
Mo	molybdenum
MPOB	Malaysian Palm Oil Board
mRNA	messenger ribonucleic acid
MS	Murashige and Skoog
Mt	*Medicago truncatula*
MYB	myeloblastosis
N	nitrogen
Na^+	Sodium ion
NCBI	National Center for Biotechnology Information
New PLACE	Plant cis-acting Regulatory DNA Elements
$(NH_4)_6Mo_7O_{24}$	Ammonium heptamolybdate
Ni	nickel
Nt	*Nicotiana tabacum*
OD	Optical density
Os	*Oryza sativa*
ORF	open reading frame
P	Phosphorus
P1BS	PHR binding site
PCR	Polymerase chain reaction
Pi	Phosphate
PHL	PHR1-LIKE
PHO	Phosphate
PHR	Phosphate starvation response
PHT	Phosphate transporter
PHT1	Phosphate transporter 1

PlantCARE	Plant Cis-Acting Regulatory Elements
PO_4^{3-}	Phosphate ion
PSI	Phosphate starvation induced
PSR	Phosphate starvation response
PSR1	Phosphorus starvation response 1
Pt	*Populus trichocarpa*
PUFA	Polyunsaturated fatty acids
Pv	*Phaseolus vulgaris*
PVP	Polyvinylpyrrolidone
qPCR	quantitative real-time PCR
RAV	Related to ABI3/VP1
RefSeq	Reference Sequences
RM	*Ringgit Malaysia*
RNA	Ribonucleic acid
rpm	Revolutions per minute
rRNA	Ribosomal ribonucleic acid
S	Sulfur
Sc	*Saccharomyces cerevisiae*
SDS	Sodium dodecyl sulfate
SLC17	Solute carrier family 17
Sm	*Solanum melongena*
S.O.C.	Super Optimal broth with Catabolite repression
SPX	SYG1/PHO81/XPR1
St	*Solanum tuberosum*
SULTR	Sulfate transporter
Ta	*Triticum aestivum*

TAE	Tris-acetate-EDTA buffer
TE	Tris-EDTA buffer
TFA	trans fatty acids
Tm	melting temperature
USA	United States of America
V	volt
VPT1	Vacuolar phosphate transporter 1
v/v	volume/volume
w/v	weight/volume
x *g*	relative centrifugal force
ZIP	Zinc transporter
Zm	*Zea mays*
$ZnSO_4$	Zinc sulfate

CHAPTER 1

INTRODUCTION

Phosphorus (P) is one of the macro-elements which are very essential for plant growth (Kehr, 2013). But the movement of P in the soil is very poor (Nussaume *et al*., 2011). It is the most immobile element among the macronutrients (Gu *et al*., 2010). The plant absorbs P in the form of phosphate (Pi) (Gonzalez *et al*., 2005). Pi can easily interact with other cations such as Ca, Al and Fe and can assimilate with the soil microorganisms (Sun *et al*., 2016; Tan *et al*., 2010). These create competition with the plant to acquire Pi and reduce the availability of Pi. Thus, huge amount of Pi fertilizer is applied in the plantation (Zhang *et al*., 2016). Pi rock, the main source for Pi fertilizer is predicted to be depleted in the next 40 to 70 years which if happen will cause chaotic disaster to the crop industries (Vance, 2001; Raghothama, 1999). Moreover, the excessive use of Pi fertilizer will lead to environmental problem (Obidzinski *et al*., 2012). The Pi fertilizer that leaches into the water will create water pollution such as eutrophication and acidification of water causing bad impact to the aquatic life (Saswattecha *et al*., 2015). Therefore, it is important to study the Pi regulatory mechanism to enhance the Pi uptake of plants so that the application of Pi fertilizer can be reduced.

Oil palm is one of the important crops in the world because it is the leading supplier of edible vegetable oil (Hadi *et al*., 2015; Corley, 2009). The demand for the vegetable oils is projected to reach 240 million tons in 2050 which ensure great economic value of the oil palm (Barcelos *et al*., 2015). Oil palm is also a very versatile plant because it can produce two types of oils: crude palm oil and palm kernel oil with different fatty acid profiles and different usages (Barcelos *et al*., 2015; Mba *et al.*, 2015; Basiron, 2007). Even though oil palm is the highest yielding crop per unit area in the world, it requires high fertilizer input to maintain high productivity (Sundram *et al.*, 2019; Mohidin *et al*., 2015). Hence, studies on mechanism of nutrient uptake is essential to ensure the sustainability of the palm oil production which will be very beneficial to the oil palm industry. By understanding the Pi regulatory mechanism in the oil palm, oil palm variety with high efficiency in Pi uptake can be developed. The increase in Pi uptake efficiency can reduce the Pi fertilizer usage and reduce the expenditure on fertilizer. The reduction of Pi fertilizer usage also can lessen the possibility of Pi fertilizer leaching thus, avoiding the environmental issues regarding oil palm plantations.

To understand the Pi regulation, the key genes involved in Pi uptake must first be discovered. The transporter protein that is responsible for the acquisition of Pi into the plant is phosphate transporter 1 (PHT1) (Qin *et al*., 2012; Muchhal *et al*., 1996). PHT1 family members are H^+/Pi symporter type of transporter localized in the plasma membrane (Fan *et al*., 2013; Loth-Pereda *et al*., 2011). The regulation of *PHT1* genes are controlled by phosphate starvation response (PHR) (Bustos *et al*., 2010; Yang & Finnegan, 2010). PHR is the transcription factor that regulates numerous Pi starvation inducible (PSI) genes (Bari *et al*., 2006). PHR regulate the genes by binding to the PHR binding site (P1BS) motif (Rubio *et al*., 2001). P1BS motif (GNATATNC) is present in

the promoter region of most of PSI genes including the *PHT1* genes (Wang *et al*., 2013). PHR proteins have been identified in many important crops. Presently, one *PHR* gene is identified in rapeseed (*Brassica napus*) (Ren *et al*., 2012), one in bean (*Phaseolus vulgaris*) (Valdes-Lopez *et al*., 2008), one in corn (*Zea mays*) (Wang *et al*., 2012), three in wheat (*Triticum aestivum*) (Wang *et al*., 2013), four in rice (*Oryza sativa*) (Ruan *et al*., 2017; Guo *et al*., 2015; Zhou *et al*., 2008) and 35 in soybean (*Glycine max*) (Xue *et al*., 2017). Thus, it is really necessary to identify the *PHR* genes in oil palm so that the scientific knowledge of Pi regulatory mechanism in this major producer of edible vegetable oil plant is not left behind compared to the other crops.

Hence, the objectives of this study are:

1) To identify and perform molecular characterization of the *PHT1* and *PHR* gene families in oil palm genome using the bioinformatics approach.
2) To profile the expression of the different *PHT1* and *PHR* genes under Pi sufficient, low Pi and Pi deficient conditions.
3) To determine the specific location of EgPHR2 protein using the subcellular localization technique.

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Muhammad Luqman bin Hamzah was born on 11th January 1993 in Tawau, Sabah. The third from six siblings, he received his early education at TASKI ABIM Seksyen 28, Shah Alam in 1999. Then he entered his primary schools at Sekolah Kebangsaan Taman Alam Megah from 2000 to 2002 and Sekolah Kebangsaan Puncak Alam from 2003 to 2005. He also received his Islamic primary education at KAFA Integrasi As-Sufla from 2000 to 2002 and KAFA Integrasi Puncak Alam from 2003 to 2005. He continued his secondary education at Sekolah Menengah Kebangsaan Puncak Alam from 2006 until 2010. He then pursued his study at Kolej Matrikulasi Pulau Pinang from 2011 to 2012. In 2012, he continued his tertiary education at Universiti Sains Malaysia (USM) and successfully graduated with a Bachelor Degree (Honours) in Plant Science in 2015. At USM, he also joined Reserve Officers Training Units and commissioned as Young Officer of Territorial Army Regiment in 2015. In 2016, he enrolled as a full-time Master candidate in the field of Plant Biotechnology at Universiti Putra Malaysia.

LIST OF PUBLICATIONS

Journals

Ahmadi, F., Abdullah, S. N. A., Kadkhodaei, S., Ijab, S. M., **Hamzah, L.**, Aziz, M. A., Rahman, Z. A., and Alwee, S. S. R. S. (2018). Functional characterization of the gene promoter for an *Elaeis guineensis* phosphate starvation-inducible, high affinity phosphate transporter in both homologous and heterologous model systems. *Plant Physiology and Biochemistry*, *127*: 320-335.

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Poster Paper Presentations

Hamzah, M. L., Abdullah, S. N. A., and Azzeme, A. M. (2017). *Transcriptional Regulation of PHT 1 Involved in Phosphate Deficiency Response in Oil Palm.* Paper presented at the International Conference on Big Data Applications in Agriculture, Serdang.

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