ISOLATION, CHARACTERISATION AND FUNCTIONAL ANALYSIS OF ROOT-SPECIFIC PROMOTERS FROM MINING OF OIL PALM TRANSCRIPTOME DATA

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 Doctor of Philosophy

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Chairman : Noor Azmi bin Shaharuddin, PhD
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Root-specific promoter is a valuable genetic engineering tool to improve oil palm resistance to diseases, malnutrition, or abiotic stresses that cause extensive losses in the oil palm industry. Since the availability of root-specific promoters from oil palm is still limited, this study was conducted to identify and characterise a strong promoter in a strict root-specific or preferential manner that may have great potential for root-system modification. Mining the transcriptome of various oil palm tissue-specific data generated from RNA Sequencing technology has resulted in discovering seven candidate genes for root-specific promoters. The expression pattern of these candidate genes was further validated through real-time quantitative polymerase chain reaction (RT-qPCR) analysis using various oil palm tissues, including root tissues at different developmental stages. Two transcripts, namely RSP-2 and RSP-3, that showed high expression in roots were selected for further research. RSP-2, annotated as an oil palm metallothionein gene (*EgMT),* was significantly

upregulated at 7 to 170-fold in roots. Likewise, RSP-3, which belongs to the proline-rich protein (*EgPRP1)* gene, was significantly upregulated at 7 to 55-fold. DNA vectors carrying a full-length promoter region and 5' promoter deletion fragments were constructed for the promoter functional study. Deletion analyses were performed according to the density of the cis-acting elements related to the root expression present in the promoter sequences. The promoter activity in transient expression was studied using the biolistic method in various oil palm tissues. The study indicated that *EgPRP1* and *EgMT* promoters could drive the expression of red fluorescence protein (DsRED) in oil palm root tissue. Since oil palm transformation was hampered by a long regeneration time, the stable promoter functional study was investigated further using tobacco as a model plant. The promoter activity was evaluated in seedlings, vegetative and reproductive tissues of T_1 generation using GUS histochemical assay. Promoter activity was evaluated based on the intensity of blue GUS staining. The RSP-3A construct (2000 bp upstream of *EgPRP1* start codon) showed root-preferential or dominant promoter activity in all the root developmental stages. Fine dissection revealed that the shortest promoter construct, designated as RSP-3D (665 bp upstream of *EgPRP1* start codon), conferred root-specific expression in mature plants. For *EgMT,* only the RSP-2D (1107 bp upstream of *EgMT* start codon) deletion construct directed strong GUS expression from early to mature root developmental stages. GUS expression directed by RSP-2A and RSP-2C constructs were detected in the roots of mature plants, with intensities lower than RSP-2D. However, the activity of *EgMT* promoters was also detectable in seed pods and immature seeds, albeit at lower levels than the *Cauliflower Mosaic Virus*

35S promoter (*CaMV35S)*. Interestingly, the GUS expression driven by RSP-3A, RSP-2C and RSP-2D was detected at the flower and leaf-cutting sites, suggesting the promoters' activity was inducible by wounding. Results also showed that the promoters consist of cis-acting elements that act as negative regulators, which might be responsible for root specificity. The results further indicated that the 5' UTR and ATATT sequences defined as ROOTMOTIFAPOX1 cis-acting elements are essential for strong promoter activity. Overall, the functional study conclusively demonstrated that the genes identified through the mining of transcriptome data and RT-qPCR analysis that were upregulated during root developmental stages have a high potential to regulate a strong expression of transgenes in a root-specific or preferential manner. The results suggest that promoter regions of RSP-3A and RSP-3D from *EgPRP1* and RSP-2D from *EgMT* are potentially helpful in facilitating oil palm genetic engineering, notably improving crop yield through root-traits modification.

Keywords: Root-specific promoter, root-preferential promoter, expression study, oil palm, tobacco

SDG: GOAL 2: Zero hunger, GOAL 12 : Responsible consumption and production.

Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Doktor Falsafah

PEMENCILAN, PENCIRIAN DAN ANALISIS FUNGSIONAL PROMOTER SPESIFIK-AKAR DARIPADA PERLOMBONGAN DATA TRANSKRIPTOM SAWIT

Oleh

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Promoter spesifik-akar merupakan alat kejuruteraan genetik yang penting bagi meningkatkan ketahanan sawit terhadap penyakit, kekurangan nutrien atau tekanan abiotik yang mana menyebabkan kerugian besar dalam industri sawit. Memandangkan ketersediaan promoter spesifik akar daripada sawit masih terhad, kajian ini dijalankan dengan objektif untuk memencilkan kawasan promoter yang kuat dengan ciri spesifik atau dominan dalam tisu akar serta berpotensi untuk digunakan dalam pengubahsuaian sistem-akar. Perlombongan data transkriptom pelbagai tisu sawit yang dihasilkan daripada teknologi penjujukan asid ribonukleik (RNA-Seq) telah menghasilkan penemuan tujuh calon-calon gen untuk promoter spesifik-akar. Corak pengekspresan calon-calon gen ini telah dianalisis menggunakan kaedah tindak balas berantai polimerase kuantitatif masa-sebenar (RT-qPCR) dengan menggunakan pelbagai tisu sawit termasuk tisu akar pada peringkat perkembangan yang berbeza. Dua transkrip, iaitu RSP-2 dan RSP-3 yang

menunjukkan kadar pengekspresan gen yang tinggi dalam akar telah dipilih untuk kajian lanjut. RSP-2 yang yang dianotasi sebagai gen metallothionein (*EgMT*) diekspreskan dengan kadar yang tinggi dalam akar iaitu sebanyak lebih kurang 7 hingga 170 kali ganda. Begitu juga, RSP-3 yang merupakan gen proline rich protein (*EgPRP1*) diekspreskan dengan kadar yang tinggi iaitu lebih kurang 7 hingga 55 kali ganda. Vektor yang membawa jujukan penuh promoter dan serpihan 5' delesi promoter telah dibina untuk kajian fungsional. Analisis delesi dilakukan berdasarkan kepadatan elemen pengawalatur-cis yang berkaitan dengan pengekspresan spesifik-akar yang terdapat dalam jujukan promoter. Aktiviti promoter dalam pengekspresan sementara telah dikaji dalam pelbagai tisu sawit menggunakan kaedah biolistik. Kajian menunjukkan promoter *EgPRP1* dan *EgMT* mampu mengaruh pengekspresan protein berpendaflour merah (DsRED) dalam tisu akar sawit. Memandangkan tempoh regenerasi sawit tertransformasi adalah sangat panjang, kajian fungsi promoter yang stabil telah dijalankan seterusnya menggunakan tembakau sebagai tumbuhan model. Aktiviti promoter dinilai dalam sampel generasi T_1 iaitu anak benih (peringkat *in vitro*), tisu vegetatif dan tisu pembiakan secara ujian histokimia GUS. Aktiviti promoter dinilai berdasarkan intensiti biru pewarnaan GUS. Untuk promoter *EgPRP1*, rantau jujukan penuh iaitu RSP-3A (2000 bp ke hulu kodon pemula *EgPRP1*) menunjukkan keutamaan atau aktiviti yang dominan dalam semua peringkat pertumbuhan akar. Analisis delesi promoter menunjukkan rantau promoter terpendek iaitu RSP-3D (665 bp ke hulu kodon pemula *EgPRP1*) mengaruh pengekpresan gen secara spesifik-akar di peringkat pokok yang matang. Untuk promoter *EgMT*, didapati hanya delesi konstruk RSP-2D (1107 bp ke

hulu kodon pemula *EgMT*) mampu mengaruh pengekspresan GUS dalam akar dari mula peringkat awal perkembangan hingga pokok matang. Pengkspresan GUS yang diaruh oleh rantau jujukan penuh iaitu RSP-2A dan jujukan delesi RSP-2C dikesan dalam akar pokok matang, dengan intensiti yang lebih rendah berbanding promoter RSP-2D. Walau bagaimanapun, aktiviti promoter *EgMT* juga dapat dikesan dalam pod benih dan benih tidak matang, dengan tahap intensiti yang lebih rendah berbanding promoter promoter *Cauliflower Mosaic Virus 35S* (*CaMV35S)*. Menariknya, pengekspresan GUS yang diaruh oleh promoter RSP-3A, RSP-2C dan RSP-2D juga dikesan di kawasan pemotongan bunga dan daun, menunjukkan aktiviti promoter boleh diaruh dengan rangsangan kecederaan. Hasil kajian menunjukkan kehadiran elemen-cis yang berfungsi sebagai pengawalatur negatif, yang mungkin bertanggungjawab untuk aktiviti spesifik akar. Keputusan juga mendapati kawasan 5’ tidak diterjemahkan (5’ UTR) dan jujukan ATATT yang ditakrifkan sebagai elemen-cis ROOTMOTIFAPOX1 adalah penting untuk aktiviti promoter yang kuat dalam akar. Secara keseluruhannya, kajian fungsional menunjukkan gen yang dikenalpasti melalui perlombongan data transkriptom dan (RT-qPCR), yang mempunyai kadar pengekspresan yang tinggi di setiap peringkat perkembangan akar berpotensi untuk mengaruh pengekspresan transgen yang kuat dalam tisu akar sama ada secara spesifik atau dominan. Keputusan menunjukkan bahawa promoter RSP-3A dan RSP-3D daripada *EgPRP1* dan RSP-2D daripada *EgMT* berpotensi membantu dalam kejuruteraan genetik sawit, terutamanya untuk meningkatkan hasil tanaman melalui pengubahsuaian trait-akar.

Kata kunci : Promoter spesifik-akar, Promoter dominan-akar,kajian pengekspresan, sawit, tembakau

SDG: MATLAMAT 2 : Kelaparan sifar, MATLAMAT 12 : Penggunaan dan penghasilan yang bertanggungjawab.

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Date: 10 October 2024

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LIST OF ABBREVIATIONS

5' RACE	5' Rapid amplification of cDNA ends
5'UTR	5′- untranslated region
A	Adenine
AtNRT2.1	*Arabidopsis thaliana* nitrate transporter 2
BA	6-Benzyladenine
bar	Bialaphos resistance gene
BLAST	Basic Local Alignment Search Tool
BLASTN	Basic Local Alignment Search Tool (nucleotide-nucleotide)
BLASTX	Basic Local Alignment Search Tool (translated nucleotide-protein)
bp	base pair
BSR	Basal stem rot
$CaCl_2$	Calcium chloride
CAGE	Cap analysis gene expression
CaMV35S	Cauliflower Mosaic virus 35S promoter
CaWRKY31	WRKY protein
CcHyPRP	Hybrid-proline-rich protein
cDNA	complementary DNA
CIAP	Calf intestinal alkaline phosphatase
CPO	Crude palm oil
Cq	Cycle quantification
Ct	Cycle threshold
CTAB	Cetyl trimethylammonium bromide
DAG	Days after germination

DHS	DNas1 hypersensitive
DNA	Deoxyribonucleic acid
dNTP	Deoxynucleotide triphosphate
DsRED	Red fluorescent protein gene
dsRNA	Double strand RNA
DTT	Dithiothreitol
EDTA	Ethylenediaminetetraacetic acid
EgMT	*Elaeis guineensis* metallotheionein
EgPHT1	High-affinity phosphate transporter
EgPRP1	*Elaeis guineensis* proline-rich protein
EST	Expressed sequence tag
ETBR	Ethidium bromide
FFB	Fresh fruit bunches
FPKM	per million mapped reads
GFP	Green fluorescent protein
GmPRP2	*Glycine max* proline rich protein
GmTIP	*Glycine max* tonoplast Intrinsic protein
GRAS	Gibberellin-responsive protein 2
GSPs	Gene-specific primers
GUS	β-glucuronidase gene
H_20_2	Hydrogen peroxidase
HTS	High-throughput sequencing
J1-1	Pepper defensin
Kb	Kilo base
KCl	Potassium chloride
LB	Luria-Bertani

LiCl	Lithium Chloride
LjNRT2	*Lotus japonica* nitrate transporter 2
MES	2-(N-morpholino)ethanesulfonic acid
$MgCl_2$	Magnesium chloride
$MgSO_4$	Magnesium sulfate
MPOB	Malaysian Palm Oil Board
mRNA	Messenger RNA
MS	Murashige and Skoog
MsPRP2	*Medicago sativa* proline rich protein
MT	Metallothionein
MT3-B	Oil palm metallothionein type 3
NAA	1-Naptheleneacetic acid
NaCl	Sodium chloride
$NaPO_4$	Sodium Phosphate
nptII	Neomycin phosphotransferase II
NRRS	Nematode-responsive root-specific
NtREL1	Extensin-like protein
OD	Optical density
ORF	Open reading frame
OsGRP7	*Oryza sativa* glycine rich-protein 7
PCR	Polymerae chain reaction
PEG	Polyethylene-glycol
PHT1	Phosphate transferase
Pht1;1	*Hordeum vulgae* phosphate transferase
pPRP3	*Arabidopsis thaliana* proline rich protein
PR10	*Pinus monticola Dougl. ex*. D. Don pathogenesis-related protein

psi	Pounds per square inch
PsPR10	*Pinus strobus* pathogenesis-related protein
PVP	polyvinylpyrrolidone
Pyk10	*Arabidopsis thaliana* myrosinase
RCc3	HPS-like protein
RDA	Representational difference analysis
RFP	Red fluorescent protein
RNA	Ribonucleic acid
RNAi	RNA interference
RNA-Seq	Ribonucleic acid sequencing
RQN	RNA Quality Number
RT-qPCR	Real-time quantitative polymerase chain reaction
SAGE	Serial analysis of gene expression
SDS	Sodium dodecyl sulfate
SLU7	Pre-mRNA-splicing factor gene
SMRT	Single Molecule Sequencing Real Time
SSH	Subtractive hybridisation
TAE	1×Tris–Acetate EDTA
TE	Tris EDTA
TFBS	Transcription factor binding sites
TIP2-2	Tonoplast Intrinsic Protein
TobRB7	*Nicotiana tabacum* tonoplast intrinsic protein
Tris-HCl	TRIS Hydrochloride
TRs	Tandem repeats
TSS	Transcription start sites

UTR	Untranslated region
WAA	Week after anthesis
X-gal	5-Bromo-4-chloro-3-indolyl β-D-galactopyranoside
X-gluc	5-Bromo-4-Chloro-3-Indolyl-β-D-glucuronide
YEB	Yeast Extract Beef

CHAPTER 1

INTRODUCTION

Root is a below-ground part of a plant that provides support and firm soil anchorage. The roots absorb water and essential nutrients for plant growth. As they interact symbiotically with organisms, roots are also prone to attack by microbial pathogens that cause soil-borne diseases. The plant root system is also sensitive to environmental stimuli such as drought, salinity, and climate change. Soil-borne disease and the uncertainties of climate change could disrupt the root systems in absorbing water and nutrients (Longsaward *et al.,* 2023). The inefficient plant root system due to these factors could interfere with the plant's physiological processes and inhibit plant development, resulting in substantial losses in yield.

Oil palm (*Elaeis guineensis* Jacq*)* is a major Malaysian commodity crop threatened by soil-borne disease and climate change, resulting in substantial losses to the industry. *Ganoderma boninense,* which causes basal stem rot disease (BSR), develops from airborne spores and spreads in the soil through the roots (Naher *et al.,* 2013; Jazuli *et al.,* 2022). It is difficult to identify infected trees during the early stage of root disease since visible symptoms on aboveground parts appear only after the fungus has destroyed almost all of the root system (Siddiqui *et al.,* 2021; Longsaward *et al.,* 2023). BSR is also the main cause of the current oil palm tree crisis in many oil palm-producing countries, including Indonesia, Thailand, the Philippines, and Myanmar

(Zakaria, 2022). Besides, the oil palm industry also saw the effects of climate change, such as the El Nino and La Nina phenomena, that decreased crude palm oil production (Balu et al., 2018). Climate change is having an influence on agricultural crop yields as well as the frequency and severity of crop epidemic diseases all over the globe (Beddington, 2010; Stern and Stern, 2007; Ejaz *et al.,* 2023). The drastic climate change will likely influence soil properties, which in turn may affect nutrient uptake by the palms (Rival, 2017). Adopting a genetic engineering approach to modify root architecture and function leads to developing stronger and healthier root systems that help maximise oil quality and yields. The strategy was successfully adopted for a wide variety of crops (Xue *et al.,* 2016; Ramireddy *et al.,* 2018; Luo *et al.*, 2020). Genetic engineering is important for the improvement of oil palm yield since the global demand for food is estimated to increase by up to 70% by 2050 (van Dijk *et al.,* 2021), and yield improvement should be focused on the available farmland (Masura *et al.,* 2017; Rasid *et al.,* 2020). To manipulate root systems, the availability of genetic engineering tools, particularly a regulatory element or promoter region, is fundamental to ensuring the genes of interest are expressed in a root-specific or preferential manner.

A promoter regulates the expression of a gene. By using the promoter specific to the root, the targeted recombinant proteins can be expressed in almost anything related to the root-soil interface. Protection against drought, increasing tolerance to salt and nutrient uptake, or increasing resistance to root pathogens are among the benefits of using root-specific promoters (Potenza *et al.,* 2004). Several root-specific promoters have been isolated and

functionally characterised from plants, including rice (Li *et al.,* 2013), tobacco (Yamamoto *et al.,* 1991), *Arabidopsis* (Vijaybhaskar *et al.,* 2008), barley (Schünmann *et al.,* 2004), chickpea (Khandal *et al.,* 2020) and banana (James *et al.,* 2022). The efficiency of promoters is notably plant-species dependent, and the success of genetic modification also depends on its efficacious selection and use. The oil palm endogenous promoters useful for root manipulation were previously reported to be derived from Type-3 metallothionein-like (*MT3-B*) (Zubaidah and Siti Nor Akmar, 2005) and high-affinity phosphate transporter (*EgPHT1*) (Ahmadi *et al.,* 2018) genes. *MT3-B* promoter was inducible by the presence of Zn^{2+} and Fe^{2+}, while *EgPHT1* was triggered in response to Pi deficiency. Although strong inducible promoters can be a great benefit, sometimes that may limit their function in a broad application of genetic engineering. Since the published information on root-specific promoters from oil palm is still limited, discovering more root-specific promoters widens the range of promoters for genetic engineering. This is also necessary to fulfil the requirements of multiple transgenes stacking and cisgenesis technologies (Chen *et al.,* 2010a; Holme *et al.,* 2013; Masura *et al.,* 2019; Koul, 2022) to avoid gene silencing.

Numerous studies have reported that promoters beneficial for root modification are derived from root-specific or root-preferential genes (Yamamoto *et al.,* 1991; Vijaybhaskar *et al.,* 2008; Li *et al.,* 2013; Khandal *et al.,* 2020; James *et al.,* 2022). Therefore, it is hypothesised that the promoter sequences of genes that were up-regulated during oil palm root development (from *in vitro* tissue culture to field planting) could be used in genetic engineering as root-specific

promoters. Mining oil palm transcriptome data through RNA-sequencing (RNA-Seq) will accelerate gene discovery. The availability of oil genome data (Singh *et al.,* 2013) and abundant transcriptome data (Singh *et al.,* 2013; Ho *et al.,* 2016; Morris *et al.,* 2020) generated from various oil palm tissues facilitates the analysis using RNA-Seq. Among the promoters successfully identified using this approach were novel tissue-specific promoters from citrus and plum (Dasgupta *et al.,* 2020) and a root-specific promoter from peanut (Geng *et al.,* 2014).

The current study aimed to identify oil palm promoters suitable for expressing transgenes in a root-specific or preferential manner that may have great potential for oil palm's root system modification. Using specific promoters suitable for a specific target transgene is essential for fine-tuning the control of transgene expression and avoiding the disruption of normal plant growth. The root-specific promoter can be an important tool for precise gene modifications to protect and improve plants' root systems and enhance crop quality and yield. To accomplish the aim of the study, the work was carried out with four main objectives:

1. To screen and identify root-specific gene candidates from the existing oil palm transcriptome libraries.
2. To profile the expression levels of the selected genes using real-time quantitative polymerase chain reaction (RT-qPCR).
3. To isolate promoter regions and to carry out deletion promoter analyses.
4. To evaluate the activities of the promoters for stable and transient expressions in tobacco and oil palm tissues, respectively.

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