UNIVERSITI PUTRA MALAYSIA

ISOLATION AND FUNCTIONAL CHARACTERIZATION OF THE HIGH-AFFINITY PHOSPHATE TRANSPORTER, PHT1, GENE PROMOTER OF OIL PALM (Elaeis guineensis Jacq.)

FARZANEH AHMADI

IPTSM 2017 2

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By

FARZANEH AHMADI

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in Fulfillment of the Requirement for the Degree of Doctor of Philosophy

March 2017

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DEDICATION

To my dearest MOTHER and FATHER and my lovely husband, for their close cooperation and continuous moral and financial support in this long journey.

Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfillment of the requirement for the degree of Doctor of Philosophy

ISOLATION AND FUNCTIONAL CHARACTERIZATION OF THE HIGH-AFFINITY PHOSPHATE TRANSPORTER, *PHT1, GENE* PROMOTER OF OIL PALM (*Elaeis guineensis* Jacq.)

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Chairman: Professor Datin Siti Nor Akmar Abdullah, PhD
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Phosphorus is one of the least available elements for plant growth especially in tropical soils. The high-affinity Pi transporters are assumed to be the main system responsible for Pi uptake by plant roots. The objectives of the study were to isolate the promoter of the high-affinity phosphate transporter gene from oil palm (*EgPHT1*) and to perform functional characterization using transgenic *Arabidopsis* and transient expression assay in oil palm tissues. The third objective was to study the effects of some exogenous signals and abiotic factors on the *EgPHT1* promoter activity. Analysis of the isolated full-length *EgPHT1* promoter region (1467 bp) using PLACE and PlantCARE databases revealed the presence of a number of putative *cis*-regulatory elements associated with response to Pi and various environmental and biotic-stress signals. Under Pi deprivation, excessive quartenary roots formation was observed and the GUS activity was induced to 5.5-fold higher compared to under Pi-sufficient condition in the transiently transformed oil palm roots but no activity was observed in the leaves. In transgenic *Arabidopsis*, 29-fold greater induction of GUS expression was observed in the Pi-starved roots with no activity in other tissues. Increasing the Pi concentration from 0 to 1250 µM resulted in reduction of the GUS activity from 9109 to 315.3 pmol/min/mg protein in the transgenic plants. As the duration of Pi starvation increased from 1 to 6 days, the GUS activity increased from 660 to 9091 pmol/min/mg protein. Increasing exogenous sucrose concentration from 0.1% to 3% elevated the GUS expression from 296 to 9151.3 pmol/min/mg protein under Pi deprivation. Glucose and fructose as metabolizable sugars could induce the promoter activity, but at low level. Pi deficient inducibilty of the promoter was maintained even under high salinity up to 100 mM. Application of IAA led to strong GUS expression, but BAP suppressed the expression under Pi deprivation. Finally, progressive 5′-deletion analyses of the *EgPHT1* promoter demonstrated that the region from - 690to -1 bp as the minimal promoter is sufficient to drive root- and Pi deprivation-specific expression in transgenic *Arabidopsis*. Deletion of the promoter region containing the P1BS element significantly reduced the promoter activity in the roots. The results also suggest the probable influenced of other positive/enhancer motifs such as W-box, G-box and E-box for maximal promoter activity. While the root-specific motifs ROOTMOTIFTAPOX1 and RAV1AAT BOX are critical for its root-specific activity.

This is the first report on the high-affinity Pi transporter gene promoter of oil palm whose activity is induced exclusively in the root under low Pi. It contains the conserved elements for driving expression in both monocots and dicots and would be a potentially valuable candidate as a genetic engineering tool.

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

PENGASINGAN DAN PENCIRIAN KEFUNGSIAN PROMOTER GEN PENGANGKUT FOSFAT AFFINITI TINGGI, *PHT1* KELAPA SAWIT (*Elaeis guineensis* Jacq.)

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Fosforus adalah salah satu daripada makronutrien yang paling sukar diserapi untuk pertumbuhan pokok di dalam tanah tropika. Pengangkut Pi berafiniti tinggi dianggap sebagai sistem utama bertanggungjawab ke atas penyerapan Pi oleh akar tumbuhan. Objektif kajian ini adalah untuk memencilkan promoter gen pengangkut fosfat berafiniti tinggi dari kelapa sawit (*EgPHT1*) dan untuk membuat pencirian kefungsian menggunakan *Arabidopsis* transgenik dan esei pengekspresan transien dalam tisu kelapa sawit. Objektif ketiga adalah untuk mengkaji kesan isyarat eksogenus dan faktor abiotik ke atas aktiviti promoter *EgPHT1*. Analisis urutan lengkap promoter *EgPHT1* (1467 bp) yang dipencilkan menggunakan pangkalan data PLACE dan PlantCARE mendedahkan kewujudan sejumlah elemen yang dianggap *cis*-pengawalatur yang berkaitan dengan respons terhadap Pi dan pelbagai isyarat alam sekitar dan tekanan biotik dan pengekspresan khusus akar. Di bawah deprivasi Pi, pembentukan akar halus yang berlebihan dan aktiviti teraruh GUS yang 5.5-kali ganda lebih tinggi berbanding keadaan Pi yang mencukupi didapati di dalam akar tetapi tiada aktiviti dikesan dalam daun. Dalam *Arabidopsis* transgenik didapati 29-kali ganda lebih tinggi induksi ekspresi GUS di dalam akar yang kebuluran Pi dengan tiada pengesanan aktiviti dalam tisu yang lain. Apabila kepekatan Pi ditingkatkan dari 0 ke 1250 µM, aktiviti GUS menurun dari 9109 ke 315.3 pmol/min/mg protein dalam tumbuhan transgenik tersebut. Apabila tempoh kebuluran Pi dipanjangkan dari 1 ke 6 hari, aktiviti GUS meningkat dari 660 to 9091 pmol/min/mg protein. Peningkatan sukrosa eksogenus dari 0.1% ke 3% meningkatkan ekspresi GUS dari 296 ke 9151.3 pmol/min/mg protein dalam keadaan kebuluran Pi. Glukosa dan fruktosa sebagai gula yang boleh dimetabolisme boleh mengaruh aktiviti promoter, tetapi pada kadar rendah. Pengaruhan semasa kebuluran Pi bagi promoter ini kekal dalam kehadiran garam yang tinggi sehingga 100 mM. Aplikasi IAA membawa kepada ekspresi tinggi GUS, namun BAP menindas ekspresi semasa kebuluran Pi. Akhirnya, analisis penghapusan progresif huluan 5′ promoter *EgPHT1* menunjukkan kawasan dari -690 kepada -1 bp sebagai promoter minima yang mencukupi untuk mengarah ekspresi khusus akar dan kebuluran Pi di dalam *Arabidopsis* transgenik. Penghapusan kawasan promoter mengandungi unsur P1BS mengurangkan secara luar biasa aktiviti promoter *EgPHT1* di dalam akar. Hasil kajian juga mencadangkan aktiviti

maksima promoter ini berkemungkinan dipengaruhi oleh motif positif/penggalak seperti W-box, G-box dan E-box. Manakala motif khusus akar ROOTMOTIFTAPOX1 and RAV1AAT BOX adalah penting untuk aktiviti khusus akar. Promoter *EgPHT1* adalah promoter pertama yang dilaporkan untuk gen pengangkut Pi afiniti tinggi daripada kelapa sawit yang mana aktivitinya diaruhkan secara eksklusif dalam akar di bawah Pi rendah. Ia mengandungi unsur terpelihara untuk mengarah ekspresi dalam kedua monokot dan dikot dan berpotensi sebagai calon untuk kegunaan dalam kejuruteraan genetik.

ACKNOWLEDGEMENTS

I wish to express my deepest endless thanks to God who made it possible to complete another step of my life and best regards from God to the last Prophet, Mohammad and his family.

I would like my deepest gratitude to the numerous people who have walked with me along the journey of this thesis. First and foremost, I would like to express my deep gratefulness to my supervisor Prof. Datin Dr. Siti Nor Akmar Abdullah for her kind support, critical advice, encouragement, suggestionsand direction throughout my research and preparation of this thesis.

I also wish to extend my sincere gratitude and appreciation to my supervisory committee, Assoc. Prof. Dr. Maheran Abdul Azizand Prof. Dr. Zaharah A. Rahman for her guidance, understanding, encouragement and supervision throughout the preparation and completion of this thesis. I would also like to express my gratitude towards Assoc. Prof. Dr. Halimi Mohd Saud and Mr Azmi Abdul Rashid for their kind support, cooperation and permission to work in their laboratory.

My sincere appreciation goes to all of my lab mates, staff and friends, who helped and supported me in the laboratory. Last but not the least, my heart-full gratitude and love to my parents and my loving husband Amin whose unconditional support, patience and understanding made this dream come true for me.

I certify that a thesis Examination Committee has met on ---------- to conduct the final examination of Farzaneh Ahmadi on her thesis entitled "Isolation and Functional Characterization of Phosphate-Starvation-Inducible *PHT1* Promoter from Oil Palm in a Transient Assay System and Transgenic *Arabidopsis Thaliana*" in accordance with the Universities and College Act 1971 and the constitution of the University Putra Malaysia [P.U.(A)106] 15 March 1998. The committee recommends that the student be awarded the doctor of philosophy.

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LIST OF ABBREVIATIONS

bp	Base pair
CaMV35S	35S promoter from cauliflower mosaic virus
CDNA	Complementary DNA
DNA	Deoxyribonucleic acid
dNTP	Deoxyribonucleoside triphosphate
E.coli	*Escherichia coli*
EDTA	Ethylenediaminether tetra-acetic acid
GSP	Gene-specific primer
Kb	Kilobase pair
PCR	Polymerase chain reaction
g	Gravity

CHAPTER 1

INTRODUCTION

Oil palm (*Elaeis guineensis* Jacq.) is a tropical plant belonging to the *Aracaceae* family with its origin in West Africa. It is now grown in more than 20 countries in South Asia, Africa and South America (Dransfield *et al.*, 2005). It is the second most important oil crop next to soybean and is poised to become the dominant oil crop early in the new decade (Sheil *et al.*, 2009). Producing 17.32 million tonnes of crude palm oil on about 5.74 million hectares of land in 2016, Malaysia is now the second greatest producer after Indonesia and the largest exporter of palm oil in the world (MPOB, 2014). Palm oil is mainly used for edible and industrial purposes such as for deep fat frying, margarine, biofuels, cosmetics, soap, detergents and surfactants (Murphy, 2007).

With the rapid expansion of the world's population, per-capita oil and fat consumption is likely to increase tremendously and the oil palm being the most productive and profitable oil crop will continue to expand in its cultivation in tropical and subtropical regions to meet this demand. Oil palm is recognized as having a high requirement for nutrients due to its high dry matter production (Goh *et al.*, 2009). However, the low fertility of highly weathered tropical soils needs to be paid greater attention for sustainable oil palm cultivation.

Phosphorus (P) is an essential macronutrient for plant growth and development. Although it is an abundant nutrient in the rhizosphere,it is largely immobile and inaccessible for assimilation by plants. This is due to its tendency to associate strongly with positively charged cations such as Fe and Al, which are plentiful in acidic tropical and subtropical soils and consequently, limits plant growth and crop yield (Sanchez *et al.*, 1997; Sanchez and Uehara, 1980). A common agricultural solution to this problem is to enrich the soil with Pi-containing fertilizers. Generally, phosphate is applied in the form of phosphate rocks at the rate of 1.0-1.25 kg per palm per year (Mutert *et al.*, 1999). However, the use of Pi fertilizers is unsustainable and may cause pollution. Hence, there is a need to develop crops that either acquire Pi or use Pi more efficiently, so that agriculture will be more sustainable with less required Pi fertilizers.

To cope with growth under low Pi availability, plants have developed a number of morphological, physiological, biochemical and molecular adaptive strategies aimed at conservation of use or enhancement of acquisition of Pi (Jain *et al.*, 2007; Raghothama, 1999; Vance *et al.*, 2003). One of the best-conserved adaptations of plants to low Pi supply is the induced expression of high-affinity Pi transporter genes. These are known as *PHT1* transporters to distinguish them from the low-affinity Pi transporters which are in the *PHT2* family. Structurally, the *PHT1* transporters are integral membrane-spanning segments linked by a hydrophilic region (Schachtman *et al.*, 1998; Smith *et al.*, 2000). Several high-affinity Pi transporters have been identified in some important crops such as rice, barley, wheat, maize, tomato and potato (Gordon-Weeks *et al.*, 2003; Nagy *et al.*, 2006; Paszkowski *et al.*, 2002; Rae *et al.*, 2003). Among the *PHT1*genes examined

so far, many are either exclusively or predominantly expressed in root tissues under Pi deficiency, consistent with the role in the uptake of Pi from the soil solution (Raghothama and Karthikeyan, 2005; Schünmann *et al.*, 2004a; Xiao *et al.*, 2006). However, expression of some of the *PHT1* genes in other organs such as stem, leaves, flowers and pollen grains indicate that *PHT1* proteins are involved not only in Pi acquisition from soil but also in distribution between different organs and remobilization within the plant (Liu *et al.*, 1998; Mudge *et al.*, 2002; Rae *et al.*, 2003).

Transcriptional activation of Pi transporters in response to Pi starvation seems to be a major regulatory mechanism for Pi uptake (Jain *et al.*, 2012; Raghothama, 2000). An effective approach to study transcriptional regulation is to monitor the activity of reporter genes driven by the specific gene promoters (Karthikeyan *et al.*, 2002). Previous studies have demonstrated that the isolated phosphate transporter genes contain *cis*-acting elements within their promoter sequences for the binding of specific transcription factors to enable them to be regulated in a tissue-specific and Pi-dependent fashion (Miao *et al.*, 2009; Schünmann *et al.*, 2004a; Tittarelli *et al.*, 2007).

Although some high-affinity phosphate transporter (*PHT1*) promoters have been isolated from different dicot and monocot plant species, especially model plants, and their regulatory functions well characterized (Miao *et al.*, 2009; Mudge *et al.*, 2002; Tittarelli *et al.*, 2007), they have not been studied in oil palm yet. Additionally, there is no report on the functional characterization of the promoter of the high-affinity phosphate transporter (*EgPHT1*) gene isolated from oil palm. Studies on the molecular mechanism for phosphate uptake is important for oil palm as it is usually grown in acidic tropical soils with low bioavailability of Pi which is a major problem limiting crop productivity.

Hence, the main aims of this study were:

1) To isolate the promoter of the high-affinity phosphate transporter gene (*EgPHT1*) from oil palm and identify the putative *cis*-regulatory elements involved in inducible activity of the promoter under phosphate deficiency.
2) To evaluate the root-specific activity of the *EgPHT1* promoter activity using a transient biolistic-based reporter assay in transformed oil palm tissues and transgenic *Arabidopsis.*
3) To analyse the functionality of the *EgPHT1* promoter in response to Pi signals including different concentrations of Pi, duration of Pi deficiency and Pi replenishment.
4) To analyse the induction of the *EgPHT1* promoter in response to some exogenous signals including sucrose, other nutrients (iron, potassium and nitrogen), phytohormones (auxin and cytokinin), light conditions and salinity.
5) To determine the promoter sequences necessary for *EgPHT1* expression in transgenic *Arabidopsis thaliana* using 5' deletion analysis.

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