UNIVERSITI PUTRA MALAYSIA

MOLECULAR CLONING AND CHARACTERIZATION OF NITRIC OXIDE ASSOCIATED 1 TRANSCRIPT FROM OIL PALM (Elaeis guineensis Jacq.) AND ITS RECOMBINANT PROTEIN PRODUCED FROM PROKARYOTIC SYSTEM

KWAN YEE MIN

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By

KWAN YEE MIN

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November 2014

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Basal stem rot (BSR) disease in oil palm is caused by *Ganoderma* fungi. It has resulted in severe economic loss, and the current disease management strategies were of low effectiveness. Nitric oxide (NO) is a ubiquitous signaling molecule which plays a role in plant disease resistance against pathogens. Nitric oxide associated 1 (NOA1) protein is implicated in NO biosynthesis and NO associated plant defense responses against pathogen infection. This study was conducted to isolate a transcript encoding NOA1 protein from oil palm (designated as *EgNOA1*) and examine the guanosine triphosphate (GTP) hydrolysis activity of its recombinant protein obtained from *Escherichia coli* (*E. coli*). In addition, the expression profile of *EgNOA1* in *Ganoderma* infected oil palm and its correlation with NO biosynthesis were investigated. The full length complementary DNA (cDNA) sequence of *EgNOA1* was isolated by Rapid Amplification of cDNA Ends Polymerase Chain Reaction (RACE PCR). *EgNOA1* has an open reading frame (ORF) of 1674 bp that encodes a polypeptide chain of 558 amino acid residues. *EgNOA1* is a circularly permuted GTPase (cpGTPase) belonging to the YqeH subfamily with three characteristic domains- zinc binding domain (ZBD), circularly permuted GTPase (CPG) domain and C-terminal domain (CTD). The motif residues of the CPG domain arranged in the permuted order are G4 (TKID), G5 (SSK), G1 (GSANVGKS), G2 (T), and G3 (DTPG). Two recombinant proteins, a complete ORF of *EgNOA1* (*EgNOA1*^{fl}) and a deletion variant (*EgNOA1*$^{\Delta 99}$) without its 99 amino acids at the N-terminal end was produced in *E. coli* cells using the pET-32 Xa/LIC expression vector and verified by Western blot analysis. The hydrolysis of GTP to guanosine diphosphate (GDP) and inorganic phosphate ion catalyzed by the purified *EgNOA1*^{fl} and *EgNOA1*$^{\Delta 99}$ recombinant proteins was measured using the malachite green assay. The purified *EgNOA1*$^{\Delta 99}$ recombinant protein was demonstrated to catalyze significantly higher release of GDP and phosphate ion compared to that of *EgNOA1*^{fl}. Griess assay and quantitative real-time PCR (qPCR)

was performed to examine the NO concentration and the expression of *EgNOA1* respectively in *Ganoderma*-treated root tissue at 3, 7, 14, 21, 28, 56 and 96 days after inoculation (DAI). NO burst was detected at 14 DAI, and the transcript abundance of *EgNOA1* was up-regulated at 96 DAI. In conclusion, the findings of this study have provided insights on *EgNOA1* as a GTPase and its differential transcript regulation in oil palm root tissue when infected by *Ganoderma*.

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

PENGKLONAN MOLEKUL DAN PENCIRIAN TRANSKRIP NITRIK OXIDA BERKAITAN 1 DARI KELAPA SAWIT (*Elaeis guineensis* Jacq.) DAN PROTEIN REKOMBINAN YANG DIHASILKAN DARIPADA SISTEM PROKARIOT

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Penyakit reput pangkal batang dalam kelapa sawit adalah disebabkan oleh kulat *Ganoderma*. Ia menyebabkan kerugian ekonomi yang besar dan strategi pengurusan penyakit pada masa kini adalah keberkesanan rendah. Nitrik oksida (NO) merupakan molekul isyarat yang memainkan peranan dalam daya rintangan tumbuhan terhadap patogen. Protein berkaitan nitrik oksida 1 (NOA1) terlibat dalam biosintesis NO dan pertahanan tumbuhan yang berkaitan dengan NO terhadap jangkitan patogen. Kajian ini adalah untuk memencil dan menganalisis transkrip yang mengekod NOA1 protein dari kelapa sawit (digelar sebagai *EgNOA1*) dan mengkaji aktiviti hidrolisis guanosine trifosfat (GTP) protein rekombinan yang dihasilkan daripada *Escherichia coli* (*E. coli*). Selain itu, profil pengekspresan *EgNOA1* dalam anak pokok kelapa sawit yang dirawat dengan *Ganoderma* dan korelasinya dengan biosintesis NO telah dikaji. Satu jujukan penuh cDNA yang mengekod protein NOA1 telah dipencilkan dengan menggunakan RACE PCR. *EgNOA1* mempunyai 1674 bp bingkai bacaan terbuka (ORF) yang mengekod rantai polipeptida yang sepanjang 558 asid amino. *EgNOA1* merupakan circularly permuted GTPase (cpGTPase) yang tergolong dalam subfamili YqeH dengan 3 domain khas- zinc binding domain (ZBD), circularly permuted GTPase (CPG) domain and C-terminal domain (CTD). Motif dalam domain CPG yang disusun mengikut turutan adalah G4 (TKID), G5 (SSK), G1 (GSANVGKS), G2 (T) dan G3 (DTPG). Dua protein rekombinan, ORF jujukan penuh *EgNOA1* (*EgNOA1*^{fl}) dan varian yang tanpa 99 asid amino di N-terminal (*EgNOA1*$^{\Delta 99}$) dihasilkan dalam sel *E. coli* dengan menggunakan vektor pET-32 Xa/LIC dan telah disahkan oleh Western blot. Hidrolisis GTP kepada guanosine difosfat (GDP) dan ion fosfat bukan organik yang dimangkin oleh protein rekombinan *EgNOA1*^{fl} dan *EgNOA1*$^{\Delta 99}$ telah diuji dengan menggunakan analisis malachite green. Protein rekombinan *EgNOA1*$^{\Delta 99}$ telah memangkin pembebasan GDP dan ion fosfat yang lebih tinggi berbanding dengan *EgNOA1*^{fl}. Analisis Griess dan PCR quantitatif masa nyata (qPCR) telah dijalankan untuk mengkaji kepekatan

NO dan pengekspresan *EgNOA1* dalam tisu akar anak pokok kelapa sawit yang dirawat dengan *Ganoderma* pada 3, 7, 14, 21, 28, 56 dan 96 hari selepas inokulasi (DAI). Pencetusan NO telah dikesan pada 14 DAI dan transkrip *EgNOA1* didapati meningkat pada 96 DAI. Sebagai kesimpulannya, hasil kajian ini telah memberi gambaran mengenai *EgNOA1* merupakan enzim GTPase dan pengekspresan transkrip *EgNOA1* dalam tisu akar kelapa sawit apabila dicabar oleh *Ganoderma*.

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For any errors and inadequacies that may remain in this work, the responsibility is entirely my own.

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

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LIST OF ABBREVIATIONS

°C	degree Celsius
aa	amino acid
AtNOA1	*Arabidopsis thaliana* nitric oxide associated 1
BLAST	basic local alignment search tool
bp	base pair
BSA	bovine serum albumin
BSR	basal stem rot
$CaCl_2$	calcium chloride
cDNA	complementary deoxyribonucleic acid
cm	centimetre
C_q	quantification cycle
CTD	C-terminal domain
DAF	diaminofluorescein
DAI	day after inoculation
DEPC	diethylpyrocarbonate
DNA	deoxyribonucleic acid
DNase I	deoxyribonuclease I
dNTPs	deoxyribonucleotide triphosphates
DTT	dithiothreitol
E. coli	*Escherichia coli*
EDTA	ethylenediaminetetraacetic acid
EPR	electron paramagnetic resonance
EST	expressed sequence tag
IB	inclusion bodies
IPTG	isopropyl-β-thio-D-galactopyranoside
g	gram
GAPDH	glyceraldehyde-3-phosphate dehydrogenase

GAPs	GTPase activating proteins
GDIs	guanidine nucleotide dissociation inhibitors
GEFs	guanidine nucleotide exchange factors
GSP	gene specific primer
GTP	guanosine triphosphate
h	hour
HAS	hydrophobic amino acid substituted for catalytic glutamine residue GTPases
JA	jasmonic acid
kDa	kilo Dalton
kg	kilogram
pI	isoelectric focusing point
kb	kilo base pair
LB	Luria-Bertani
LIC	ligation independent cloning
LiCl	lithium chloride
M	molar
MEA	malt extract agar
MEGA	Molecular Evolutionary Genetics Analysis
MIQE	minimum information for publication of quantitative Real-time PCR experiment
min	minute
miRNAs	microRNAs
mL	milliliter
mM	milimolar
M-MuLV	Moloney murine leukemia virus
MSD	Manganese superoxide dismutase
NaCl	sodium chloride
NAD	NADH dehydrogenase subunit 5-like
NCBI	National Center for Biotechnology Information

ng	nanogram
NGSP	nested gene specific primer
Ni-NTA	nickel-nitrilotriacetic acid
NJ	Neighbor-Joining
NO	nitric oxide
NOA1	nitric oxide associated 1
NOS	nitric oxide synthase
ORF	open reading frame
PAL	phenylalanine ammonia lyase
PAMPs	pathogen associated molecule patterns
PBS	phosphate-buffered saline
PR	pathogenesis-related
PRRs	pattern recognition receptors
PTI	PAMP-triggered immunity
RACE	rapid amplification of cDNA ends
RNA	ribonucleic acid
rRNA	ribosomal ribonucleic acid
ROS	reactive oxygen species
RWB	rubber wood block
s	second
SA	salicylic acid
SAR	systemic acquired resistance
SDS	sodium dodecyl sulphate
T_a	annealing temperature
T_m	melting temperature
TAE	tris-acetate EDTA
TCP	total cell protein
TEMED	N,N,N',N'-tetramethylethylenediamine
TRAP	tryptophan RNA-binding attenuating protein

µL	microliter
µM	micromolar
UTR	untranslated region
UV	ultraviolet
v/v	volume per volume
w/v	weight per volume
ZBD	zinc binding domain

CHAPTER 1

INTRODUCTION

1.1 Introduction

The Malaysian oil palm industry has made a substantial contribution to the national economic growth with its total export revenue of RM61.36 billion in 2013 (MPOB, 2013). The insatiable demand for edible and non-edible oil to sustain the expanding world population has further secured the future of the industry. Nevertheless, the destructive basal stem rot disease (BSR) caused by the white rot fungi, *Ganoderma* species has posed a major challenge to sustainable palm oil production.

The BSR disease has caused significant reduction in fresh fruit bunch (FFB) and collapse of standing palms costing RM225 million to RM1.5 billion annually (Idris *et al*., 2003; Chung, 2011; Hushiarian *et al*., 2013). The incidence has been consistently reported in oil palm nursery and plantation but, predominantly in former coconut plantation, coastal and replanted areas (Lim and Udin, 2010; Chung, 2011; Wong *et al*., 2012). BSR disease might paralyze the industry as the present control methods are ineffective in managing the disease, which is further aggravated by depleting agricultural land and monoculture practices in plantation that favour *Ganoderma* establishment.

The present disease management practices such as soil mounding, mechanical removal of infected tissues, trench system, sanitation during replanting, fungicide application, legume cover crops, biological control, fertilizer and biofertilizer input manage to prolong the productive years of infected palms but were not effective in disease eradication. The lack of early disease symptom, disease detection tools, and the resistance pseudosclerotia structure of the *Ganoderma* fungi are the major hindrances to an effective disease management (Naher *et al*., 2013).

Host defense is an effective, durable and economical approach in disease management. Resistance and tolerance are the two distinct classes of host defense. Resistance host inhibits infection by restricting pathogen proliferation and development whereas tolerance host is susceptible to infection, but with the ability to minimize the mortality consequences (Horns and Hood, 2012). Resistance host carrying resistance (R) genes which are involve in pathogen perception and/or onset of defense signaling network leading to incompatible interaction with the invading pathogen (Hammond-Kosack and Kanyuka, 2007). On the other hand, tolerance trait may contribute by various defense responses in pathogen associated molecule pattern (PAMP)-triggered immunity (PTI) and effector-triggered immunity (ETI) (Kawano *et al*., 2010).

The advancement in biotechnology techniques has unveiled many opportunities to augment conventional plant breeding approach towards genetic improvement program. Transformation of R genes into susceptible host plant is a genetic modification (GM) approach to increase host resistance and minimize the usage of pesticides. Breeding of BSR resistance or tolerant oil palm planting materials is of advantage to restrict disease development and/or reduce inoculum source in subsequent replanting. Oil palms from different geographical origin were reported to exhibit different susceptibility to *Ganoderma* attack (Idris *et al*., 2004; Durand-Gasselin *et al*., 2005). However, no true resistance to *Ganoderma* has been reported (Idris *et al*., 2004). Emerging effort has been given to the exploitation of defense associated genes in oil palm. These genes may be developed as biomarkers for marker-assisted breeding of tolerance oil palm progenies.

Nitric oxide (NO) has emerged as an endogenous signaling molecule affecting plant physiological processes such as seed germination, stomatal movement, leaf senescence, root organogenesis, flowering, stress tolerant, and disease resistance (Fröhlich and Durner, 2011). The NO mediated defense responses include hypersensitive response (HR), activation of salicylic acid (SA) and jasmonic acid (JA) signaling pathway, antimicrobial compound accumulation, cell wall lignification, modulation of defense related gene, and post-translational protein modification (Delledonne, 2005; Ferrarini *et al*., 2008; Leitner *et al*., 2009; Misra *et al*., 2010).

In mammalian system, nitric oxide synthases (NOSs) (EC 1.14.13.39) are the key source of NO production involving the oxidation of L-arginine to generate L-citrulline and NO (Alderton *et al*., 2001). NOSs have been reported in bacteria, fungi and green algae but not in plants. NOS-like activity has been detected in plants based on the oxidation activity of L-arginine to L-citrulline and NO (Durner *et al*., 1998; Wong, 2004). The *Arabidopsis thaliana* NO synthase 1 (*AtNOS1*) was initially identified as a novel plant NOS, but was later renamed to *A. thaliana* NO associated 1 (*AtNOA1*) (Crawford *et al*., 2006; Zemojtel *et al*., 2006). The renaming is based on the findings that indicate *AtNOA1* is a circular permuted GTPase (cpGTPase) (Zemojtel *et al*., 2006; Moreau *et al*., 2008). This is supported by the contradictory arginine-dependent NO synthesis activity of the *AtNOS1* recombinant protein and NO accumulation responses in NOA1-silenced mutants (Van Ree *et al*., 2011). The indirect contribution of NOA1 protein to NO biosynthesis is currently identified to be dependent on sucrose availability and nitrate reductase (NR)-related (Gas *et al*., 2009; Van Dee *et al*., 2011). Apart from NO biosynthesis, *AtNOA1* play roles in enhanced tolerance to abiotic and biotic stresses (Flores-Perez *et al*., 2008; Asai and Yoshioka, 2009).

In plants, extensive disease resistance studies have been conducted on small GTPase of the Ras-like superfamily and, little is known concerning the role of NOA1 protein/cpGTPase in disease resistance. The identification of defense-related genes is crucial to genetic improvement program in breeding of resistance or tolerant oil palm progenies towards *Ganoderma* through marker-assisted breeding. Therefore, this study was aimed to address the research questions that an orthologue of NOA1

gene is present in oil palm with the potential biological role as GTPase. In addition, it was hypothesized that the gene expression pattern of NOA1 is responsive to *Ganoderma* invasion and correlate with NO production in infected tissue.
This research was undertaken with the following objectives-

i) To isolate and analyze a full length cDNA encoding nitric oxide associated (NOA) protein in oil palm.
ii) To examine the GTP hydrolysis activity of *EgNOA1* recombinant protein obtained from pET prokaryotic expression system.
iii) To study the expression profile of *EgNOA1* transcript in *Ganoderma*-infected oil palm and its correlation with NO biosynthesis.

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