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MOLECULAR CHARACTERIZATION OF NADPH OXIDASE GENES AND EXPRESSION OF MarbohB1 GENE IN RESPONSE TO FUNGAL PATHOGEN Fusarium oxysporum f. sp. cubense IN BANANA

CHAI SIEW YING

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By

CHAI SIEW YING

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July 2019

Chair : Noor Baity binti Saidi, PhD
Faculty : Biotechnology and Biomolecular Sciences

Plant NADPH oxidases or also known as respiratory burst oxidase homolog (rboh) catalyzes the production of reactive oxygen species (ROS) which play crucial roles in plant development, hormone signalling and defense reactions. ROS production via plasma membrane-localized RBOHs is one of the earliest responses during pathogen infection in plants. Fusarium wilt is recognized as one of the most destructive banana diseases in the world that is caused by *Fusarium oxysporum* f. sp. *cubense* (*Foc*), a soil-borne fungus. Despite numerous reports on the involvement of ROS in *Foc*-banana interaction, *rboh* genes have not yet been identified in banana thus hindering the profiling of *Marboh*s expression in response to fusarium wilt infection. The aim of this study is to characterize *rbohs* in banana (*Marbohs*) and identify defense-related *Marbohs* through genome-wide and gene expression analysis in relation with hydrogen peroxide and electrolyte leakage level. In this study, we have identified nineteen *Marbohs* distributed on nine chromosomes of DH Pahang through database search. The functional domain organization of *Marbohs* include respiratory burst NADPH oxidase, EF-hand calcium binding domain (EFh), EF-hand domain pair (EFh-7), Nox/Duox transmembrane protein and NAD binding domain (NAD binding 6) are important for ROS production. Phylogenetic analysis clustered *Marbohs* into four subgroups and had a closer relationship with those from *Manihot esculenta, Arabidopsis thaliana* and *Brassica rapa*. Among all *Marbohs*, only *MarbohB1* is located in subgroup III where most of the *rbohs* are related with plant defense response against pathogen. Based on the digital gene expression analysis of *Marboh* transcripts, *MarbohB1* was significantly downregulated at 48 hpi and 96 hpi following *Fusarium oxysporum* f. sp. *cubense* Tropical Race 4 (*Foc*TR4) infection. Based on the phylogenetic and digital gene expression analysis, *MarbohB1* was chosen for further analysis in this study. The full length of Berangan *MarbohB1* (*MabrbohB1*) was isolated via primer walking. The amino acid alignment of DH Pahang *MarbohB1* and Berangan *MabrbohB1* revealed 13 single nucleotide polymorphisms (SNPs) which caused 6 nonsynonymous and 6 synonymous amino acid changes in which 4 nonsynonymous occurred in conserve domains. The organ-specific and temporal expression analysis of *MabrbohB1* upon hemibiotrophic fungal pathogen *Foc*TR4 infection showed that *MabrbohB1* was specifically expressed in root and exhibited a transient up-regulation after 2 hpi of *Foc*TR4 inoculation, followed by down regulation at 48 hpi and 96 hpi. The increased expression was accompanied by steady increment of H_2O_2 level and electrolyte leakage in the infected root, suggesting that *MabrbohB1* may be involved in defense responses in banana. Characterization of *Marbohs* and identification of *MarbohB1* as defense-related gene add new knowledge about *Foc*TR4-banana interaction and might be useful to counter fusarium wilt infection in the future. Overall, this research supports the suggested role of *rboh* genes in oxidative burst during plant response to pathogen.

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

PENCIRIAN MOLEKUL GEN-GEN *NADPH* OKSIDASE DAN EKSPRESI *MarbohB1* DALAM TINDAK BALAS TERHADAP PATOGEN KULAT *Fusarium oxysporum* f. sp. *cubense* DALAM PISANG

Oleh

CHAI SIEW YING

Julai 2019

Pengerusi : Noor Baity binti Saidi, PhD
Fakulti : Bioteknologi dan Sains Biomolekul

NADPH oksidase tumbuhan atau dikenali sebagai *homolog ledakan pernafasan oksidase* (*rboh*) merupakan pemangkin pengeluaran spesis oksigen reaktif (ROS) yang memainkan peranan yang penting dalam perkembangan tumbuhan, isyarat hormon dan mekanisma pertahanan. Pengeluaran ROS oleh RBOHs yang terletak di membran plasma merupakan salah satu tindakbalas yang paling awal semasa serangan patogen dalam tumbuhan. *Fusarium wilt* dikenali sebagai salah satu penyakit pisang yang paling merosakkan di seluruh dunia yang disebabkan oleh *Fusarium oxysporium* f. sp. *cubense* (*Foc*), sejenis kulat di dalam tanah. Walaupun terdapat banyak laporan tentang penglibatan ROS dalam interaksi *Foc*-pisang, walaubagaimanapun, gen *rboh* dalam pisang masih belum dikenal pasti, maka menghadkan pemprofilan expresi *Marbohs* terhadap serangan Fusarium wilt. Matlamat utama kajian ini ialah untuk mencirikan *rbohs* dalam pisang (*Marbohs*) dan mengenalpasti *Marbohs* yang berkaitan dengan pertahanan melalui analisi ekspresi gen dan genomyang dikaitkan dengan tahap hidrogen peroksida dan kebocoran elektrolit. Dalam kajian ini, sembilan belas gen *Marbohs* telah dikenal pasti dalam sembilan kromosom DH Pahang melalui pencarian pangkalan data. Organisasi domain fungsian *Marbohs* termasuk ledakan pernafasan NADPH oksidase, domain pengikat kalsium *EF-hand* (EFh), pasangan domain *EF-hand* (EFh-7), Nox/ Duox protein transmembran dan domain pengikat NAD (*NAD binding 6*) yang penting untuk pengeluaran ROS. Analisis filogenetik telah mengelompokkan *Marbohs* ke dalam empat subkelompok dan mempunyai hubungan yang lebih rapat dengan *Manihot esculenta*, *Arabidopsis thaliana* dan *Brassica rapa*. Di antara semua *Marbohs*, hanya *MarbohB1* terletak di kumpulan III yang mana kebanyakan *rbohs* terlibat dalam tindakbalas pertahanan menentang patogen. Berdasarkan analisis ekspresi gen digital transkrip *Marbohs, MarbohB1* menunjukkan penurunan

yang ketara pada 48 dan 96 jam selepas inokulasi *Foc* Tropical Race 4 (*Foc*TR4). Berdasarkan analisis filogenetik dan ekspresi gen digital, *MarbohB1* telah dipilih untuk analisis yang seterusnya. Jujukan penuh *MarbohB1* dari Berangan (*MabrbohB1*) telah dipencilkan menggunakan kaedah *primer walking*. Penjajaran asid amino *MarbohB1* dari DH Pahang dan Berangan mendedahkan 13 polimorfisme nukleotida tunggal (SNPs) yang menyebabkan 6 perubahan asid amino tanpa sinonim dan 6 perubahan asid amino sinonim di mana 4 perubahan asid amino tanpa sinonim berlaku di domain abadi. Analisa ekspresi organ dan temporal *MabrbohB1* semasa infeksi kulat hemibiotrof *Foc*TR4 menunjukkan bahawa *MabrbohB1* diekspreskan secara khusus di dalam akar dan menunjukkan peningkatan secara sementara 2 jam selepas inokulasi oleh *Foc*TR4, diikuti penurunan pada 48 dan 96 jam selepas inokulasi. Peningkatan ekspresi tersebut disertai dengan peningkatan mantap tahap H_2O_2 dan kebocoran elektrolit dalam akar yang diinokulasi, menunjukkan bahawa *MabrbohB1* mungkin terlibat dalam tindak balas pertahanan dalam pisang. Pencirian *Marbohs* dan pengenalpastian *MarbohB1* sebagai gen dalam pertahan menyumbang pengetahuan baru tentang interaksi Foc-pisang dan mungkin berguna untuk menangani penyakit *Fusarium wilt* dalam pisang pada masa akan datang. Secara keseluruhan, kajian ini menyokong peranan gen *rboh* yang dicadangkan dalam ledakan oksidatif semasa tindak balas tumbuhan dengan patogen.

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Noor Baity binti Saidi, PhD
Associate Professor
Faculty of Biotechnology and Biomolecular Sciences
Universiti Putra Malaysia
(Chairman)

Nur Fatihah Mohd Yusoff, PhD
Senior Lecturer
Faculty of Biotechnology and Biomolecular Sciences
Universiti Putra Malaysia
(Member)

Teo Chee How, PhD
Senior Lecturer
Centre for Research in Biotechnology for Agriculture (CEBAR)
Universiti Malaya
(Member)

____
ZALILAH MOHD SHARIFF, PhD
Professor and Dean
School of Graduate Studies
Universiti Putra Malaysia

Date: 18 February 2021

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

$\bullet O_2^-$	Superoxide
•OH	Hydroxyl radical
$1O_2$	Singlet oxygen
BIK1	Botrytis-induced kinase 1
bp	Base pair
Ca^{2+}	Calcium ions
cDNA	Complementary deoxyribonucleic acid
CTAB	Cetyl trimethylammonium bromide
cv.	Cultivar
DEPC	Diethyl pyrocarbonate
DNA	Deoxyribonucleic acid
DUOX	Dual oxidase
EDTA	Ethylenediaminetetraacetic acid
EF	Elongation factor
EL	Electrolyte leakage
ETI	Effector-triggered immunity
FAD	Flavin adenine dinucleotide
FAOSTAT	Food and Agriculture Organization of the United Nations statistic
Fe	Iron
Foc	Fusarium oxysporium f. sp. cubense
FW	Fresh weight
GCTCV	Giant Cavendish Tissue Culture Variants
H^+	Hydrogen ion
H_2O_2	Hydrogen peroxide
hpi	Hour post infection
HR	Hypersensitive cell death response
HWC	Hyphal wall components
K^+	Potassium ion
kb	Kilo base pair
LiCl	Lithium chloride
MAMPs	Microbe-associated molecular patterns
NaCl	Sodium chloride
NAD	Nicotinamide-adenine dinucleotide
NADPH	Nicotinamide adenine dinucleotide phosphate
NCBI	National Centre for Biotechnology Information
NLR	Nucleotide-binding leucine-rich repeat
NO	Nitric oxide
NOX	NADPH oxidase
PA	Phosphatidic acid
PAMPs	Pathogen-associated molecular patterns
PCR	Polymerase chain reaction
PDA	Potato dextrose agar
PRRs	Pathogen recognition receptors
PTI	PAMP-triggered immunity
PVP	Polyvinylpyrrolidone
RBOH	Respiratory burst oxidase homologs

RNA	Ribonucleic acid
ROI	Reactive oxygen intermediates
ROS	Reactive oxygen species
S	Sulphur
SA	Salicylic acid
SAR	Systemic acquired resistance
SNP	Single nucleotide polymorphism
SOD	Superoxide dismutase
spp	Species
SR4	Subtropical Race 4
subsp.	Subspecies
TR4	Tropical Race 4
TTSS	Type III secretion system
VCG	Vegetative compatibility group
UPM	Universiti Putra Malaysia

CHAPTER 1

INTRODUCTION

In plants, respiratory burst oxidase homologs (RBOHs) or also known as NADPH oxidase play an important role in reactive oxygen species (ROS) production. ROS are the key components for plants to carry out basic biological processes such as response to biotic and abiotic stresses as well as modulation of protein and gene expression. RBOHs are membrane-localized proteins where C-terminal consists of FAD- and NADPH-binding sites, N-terminal consists of Ca^{2+} binding EF hand motifs and six conserved transmembrane helixes in between (Liu et al., 2019). Since the discovery of the first *rboh* gene in rice (Groom et al., 1996), many *rboh genes* have been identified in other plants including *Arabidopsis thaliana* (*Arabidopsis*), tobacco, tomato and potato (Hyodo et al., 2017, Kadota, Shirasu & Zipfel, 2015; Li et al., 2015; Wang et al., 2013; Torres and Dangl, 2005). Studies on different members of *rbohs* showed that they control different biological processes in plant such as plant development, hormone signalling and defense reactions (Wang et al., 2018).

ROS production via oxidative burst is one of the earliest responses during pathogen infection. Several plasma membrane-localized RBOHs for example AtRBOHD and its orthologues are responsible for ROS production during both pathogen-associated molecular pattern-triggered and effector-triggered immunities in plants (Kadota, Shirasu & Zipfel, 2015). In addition, *rbohB* from tomato, potato, rice and tobacco also positively regulates resistance response to pathogen (Li et al., 2015; Hajianfar et al., 2016; Kosami et al., 2014; Yoshioka et al., 2003).

Fusarium wilt is recognized as one of the most destructive banana diseases in the world (Köberl et al., 2017). The disease is caused by *Fusarium oxysporium* f. sp. *cubense* (*Foc*), a soil-borne fungus. Among four *Foc* races, *Foc* Tropical Race 4 (*Foc*TR4) is the most virulent, infecting almost 80% of banana cultivars worldwide (Luo et al., 2016). In Malaysia, the losses caused by *Foc*TR4 infection was reported to be about $253 million in 2017 (FAO, 2017). The disease mostly affected banana that belongs to the AAA genome group including the famous dessert banana in Malaysia, *Musa acuminata* cv Berangan (Berangan). ROS have been reported to benefit hemibiotrophic pathogens such as *Foc*, which change from biotroph to necrotroph, stimulating the host to produce ROS or induce their own ROS production and feeding dead plant tissues to survive and reproduce. To our knowledge, *rboh* genes have not yet been characterized in banana. Thus, this study aims to identify *rboh* homologs in *Musa acuminata* subsp. Malaccensis (DH Pahang) and characterize selected *rboh* homolog in the local Berangan during a compatible interaction with *Foc*TR4. It is hypothesized that *Musa acuminata rboh* (*Marboh*) genes share a common structure with RBOH from other plants and selected *Marboh*(*s*) with predicted role in defence response is induced by *Foc*TR4.

The work described in this thesis was designed to achieve the following objectives:

1. To characterize *Marboh* genes in the resistant DH Pahang by in silico analysis
2. To isolate defense-related *Marboh* from the susceptible Berangan and analyse its expression in response to *Foc*TR4 infection
3. To determine the effect of *Foc*TR4 infection on the level of reactive oxygen species (ROS) and the extent of cell death in Berangan banana

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