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CLONING AND EXPRESSION ANALYSIS OF MANGANESE PEROXIDASE AND LACCASE TRANSCRIPTS FROM Ganoderma boninense PER71 IN RESPONSE TO DIFFERENT NITROGEN SOURCES, PHYTOHORMONES AND HYDROGEN PEROXIDE

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By

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CLONING AND EXPRESSION ANALYSIS OF MANGANESE PEROXIDASE AND LACCASE TRANSCRIPTS FROM *Ganoderma boninense* PER71 IN RESPONSE TO DIFFERENT NITROGEN SOURCES, PHYTOHORMONES AND HYDROGEN PEROXIDE

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Basal Stem Rot (BSR) is a serious disease caused by *Ganoderma* species. *Ganoderma boninense* produces lignin degrading enzymes (LDEs) that are able to degrade the lignin component of plant cell wall causing oil palms to rot and eventually collapse. The transcripts and expressions of LDEs including manganese peroxidase (MnP) and laccase (Lac) in *G. boninense* PER71 during oil palm-*Ganoderma* interaction have not been reported. Likewise, the effect of nitrogen sources in fertilizers, phytohormones and hydrogen peroxide on the growth and gene expression of *G. boninense* are unknown. Therefore, the objectives of this study were to clone the transcripts encoding these LDEs; to measure their gene expression in *G. boninense* PER71 treated with different nitrogen sources (ammonium sulphate, ammonium nitrate, sodium nitrate and potassium nitrate), phytohormones (jasmonic acid, JA and salicylic scid, SA) and hydrogen peroxide; and to evaluate the effect of different nitrogen sources on the *in vitro* growth of *G. boninense* and oil palm seedlings inoculated with *G. boninense*. The full-length cDNA of four MnPs and three Lacs were cloned from *G. boninense* by Rapid Amplification of cDNA Ends (RACE)-PCR and confirmed by sequence analysis. Real-time reverse transcription-PCR (qRT-PCR) analysis showed that only Unigene 6011 (MnP) from *G. boninense* was up-regulated by all nitrogen sources and hydrogen peroxide but down-regulated in JA treatment. Unigene 87 (MnP) showed up-regulation in *G. boninense* treated with JA. Unigene 35959 (MnP) of *G. boninense* was up-regulated by ammonium sulphate treatment, down-regulated by hydrogen peroxide and suppressed by sodium nitrate and SA. Meanwhile, Unigene 30636 (Lac) was up-regulated by SA; down-regulated by hydrogen peroxide and suppressed by ammonium sulphate, potassium nitrate and JA. Unigene 36023 (Lac) was up-regulated by JA and hydrogen peroxide while Unigene 90667 (Lac) was up-regulated by ammonium nitrate, JA, SA and hydrogen peroxide. The growth of *G. boninense* cultured on ammonium nitrate-containing Czapek-Dox agar was the fastest while the growth on sodium nitrate was the slowest based on the

measurement of radial mycelial diameter. The optical mycelial density of *G. boninense* cultured on ammonium nitrate was also denser than that of *G. boninense* cultured on sodium nitrate. However, the highest optical mycelial density was observed for *G. boninense* cultured on ammonium sulphate. On the other hand, *G. boninense*-infected oil palm seedlings treated with ammonium nitrate were the least infected; white mycelia were not observed at the basal region and root surface as compared to oil palm seedlings in other nitrogen treatments. Inoculated oil palm seedlings without additional nitrogen; treated with ammonium sulphate, sodium nitrate and potassium nitrate showed increased disease symptoms. The most serious disease symptoms were observed in oil palm seedlings without nitrogen supplement, followed by sodium nitrate and potassium nitrate, ammonium sulphate then ammonium nitrate. The results showed that ammonium nitrate is a preferable source of nitrogen for growth of *G. boninense* and could slow down BSR development. In conclusion, the study contributes to the basic understanding of the effects of different nitrogen sources, phytohormones and hydrogen peroxide on *G. boninense* and the expression of MnP and Lac, as well as the disease development of BSR in oil palm seedlings.

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

PENGKLONAN DAN ANALISIS PENGEKSPRESAN MANGANAN PEROKSIDASE DAN LAKASE DARIPADA *Ganoderma boninense* PER71 YANG BERTINDAK BALAS TERHADAP SUMBER NITROGEN YANG BERBEZA, FITOHORMON DAN HIDROGEN PEROKSIDA

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Reput pangkal batang (BSR) merupakan sejenis penyakit yang membimbangkan disebabkan oleh spesies *Ganoderma*. *Ganoderma boninense* menghasilkan enzim pereput lignin (LDE) yang boleh mereputkan komponen lignin pada dinding sel kelapa sawit menyebabkan pereputan dan seterusnya keruntuhan. Transkrip dan pengekspresan LDE termasuk manganan peroksidase (MnP) dan lakase (Lac) daripada *G. boninense* PER71 dalam interaksi kelapa sawit-*Ganoderma* belum pernah dilaporkan. Begitu juga dengan kesan sumber nitrogen dalam baja, fitohormon dan hidrogen peroksida terhadap pertumbuhan dan ekspresi gen *G. boninense* yang tidak diketahui. Oleh itu, objektif kajian ini adalah untuk mengklonkan transkrip LDE; mengukur gen ekspresi mereka dalam *G. boninense* PER71 yang telah dirawat dengan sumber nitrogen yang berbeza (ammonium sulfat, ammonium nitrat, natrium nitrat dan kalium nitrat), fitohormone tumbuhan (asid jasmonik, JA dan asid salisilik, SA) dan hidrogen peroksida; serta menilaikan kesan sumber nitrogen yang berbeza ke atas pertumbuhan *G. boninense* secara *in vitro* dan anak benih kelapa sawit yang telah diinokulasi dengan *G. boninense*. cDNA lengkap empat MnP dan tiga Lac telah diklonkan daripada *G. boninense* dengan menggunakan *Rapid Amplification of cDNA Ends (RACE)-PCR* dan dikenalpasti dengan analisis jujukan. Analisasi tindakbalas berantai polimerase-masa nyata (qRT-PCR) menunjukkan bahawa pengekspresan Unigene 6011 (MnP) telah dipertingkatkan oleh semua sumber nitrogen dan hidrogen peroksida tetapi diperturunkan dalam rawatan JA. Unigene 87 (MnP) hanya menunjukkan peningkatan pengekspresan gen dalam *G. boninense* yang dirawat JA. Gen pengekspresan Unigene 35959 (MnP) dalam *G. boninense* dipertingkatkan oleh ammonium sulfat, diturunkan oleh hidrogen peroksida dan ditindas oleh natrium nitrate dan SA. Sementara itu, pengekspresan Unigene 30636 (Lac) dipertingkatkan oleh SA; diturunkan oleh hidrogen peroksida dan ditindas oleh ammonium sulfat, kalium nitrat dan JA. Ekspresi Unigene 36023 (Lac) dipertingkatkan oleh JA dan hidrogen peroksida manakala ekspresi Unigene 90667 (Lac) dipertingkatkan dalam ammonium nitrate, JA, SA dan hidrogen peroksida. Berdasarkan pengukuran diameter jejari, pertumbuhan *G. boninense* adalah paling cepat di atas agar Czapek-Dox

yang mengandungi ammonium nitrat manakala pertumbuhan atas natrium nitrat adalah paling lambat. Kepadatan optikal mycelium *G. boninense* di atas media ditambah ammonium nitrat adalah lebih tinggi daripada *G. boninense* yang ditumbuh atas media ditambah natrium nitrat. Walau bagaimanapun, kepadatan optikal mycelium *G. boninense* adalah paling tinggi untuk *G. boninense* yang ditumbuh atas media ditambah ammonium sulfat. Selain itu, anak benih kelapa sawit yang dijangkiti dengan *G. boninense* dan dirawat dengan ammonium nitrat menunjukkan jangkitan yang paling minima; micelium tidak didapati pada kawasan pangkal dan permukaan akar berbanding dengan anak benih kelapa sawit yang dirawat dengan sumber nitrogen yang lain. Anak benih kelapa sawit yang diinokulasi tanpa penambahan sumber nitrogen; yang dirawat dengan ammonium sulfat, natrium nitrat dan kalium nitrat menunjukkan peningkatan simptom penyakit. Simptom penyakit yang paling ketara didapati pada anak benih kelapa sawit yang tidak dibekalkan sumber nitrogen tambahan, diikuti oleh anak benih kelapa sawit yang dirawat natrium nitrat, kalium nitrat, ammonium sulfat dan ammonium nitrat. Penemuan kajian menunjukkan ammonium nitrat merupakan sumber nitrogen yang sesuai untuk pertumbuhan *G. boninense* dan boleh melambatkan perkembangan BSR. Kesimpulannya, penemuan kajian ini telah menyumbang terhadap pemahaman asas tentang kesan sumber nitrogen yang berbeza, fitohormon dan hidrogen peroksida terhadap *G. boninense* dan pengekspresan MnP dan Lac, serta perkembangan simptom penyakit BSR pada anak benih kelapa sawit.

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LIST OF ABBREVIATIONS

AAO	Aryl alcohol oxidase
ANOVA	Analysis of variance
Avr	Avirulence
°C	Degree Celsius
BLAST	Basic local alignment search tool
bp	Base pair
BSA	Bovine serum albumin
BSR	Basal stem rot
CAZys	Carbohydrate active enzymes
cDNA	Complementary deoxyribonucleic acid
CDS	Coding sequence
cm	Centimeter
CWDEs	Cell wall degrading enzymes
dATP	Deoxyadenosine triphosphate
$DBQH_2$	Hydroquinone
DEPC	Diethyl pyrocarbonate
DMRT	Duncan's Multiple Range Test
DNA	Deoxyribonucleic acid
DNase	Deoxyribonuclease
dNTP	Deoxyribonucleic triphosphate
dpi	Days post inoculation
DSI	Disease severity index
DTT	Dithiothreitol
EDTA	Ethylenediaminetetraacetic acid

ELISA	Enzyme-linked immunosorbent assay
EPR	Electron paramagnetic resonance
EtBr	Ethidium bromide
G	Guaiacyl
g	Gram
GSPs	Gene specific primers
G-type	Guaiacyl type
HCL	Hydrochloric acid
H_2O_2	Hydrogen peroxide
HR	Hypersensitive response
IPTG	Isopropyl β-D-1-thiogalactopyranoside
JA	Jasmonic acid
L	Liter
Lac	Laccase
LB	Luria-Bertani broth
LDEs	Lignin degrading enzymes
LiP	Lignin peroxidase
M	Molarity
MEA	Malt extract agar
min	Minutes
mg	Milligram
ml	Milliliter
mm	Millimeter
mM	Millmolar
Mn^{2+}	Manganese
MnP	Manganese peroxidase

MPOB	Malaysian Palm Oil Board
NaCl	Sodium chloride
NCBI	National centre for biotechnology information
ng	Nanogram
NPK	Nitrogen, phosphorus and potassium
NUP	Nested universal primer A
OD	Optical density
ORF	Open reading frame
PCR	Polymerase chain reaction
PCI	Phenol:Chloroform:Isoamyl Alcohol (25:24:1, v/v)
PDA	Potato dextrose agar
PDB	Potato dextrose broth
POPW	Paddy and oil palm wood
qRT-PCR	Quantitative real-time polymerase chain reaction
R	Resistance
R^2	Correlation coefficient squared
RACE	Rapid amplification of cDNA ends
RNA	Ribonucleic acid
ROS	Reactive oxygen species
Rpm	Revolutions per minute
RT	Reverse transcription
S	Syringyl
s	Seconds
SA	Salicylic acid
SDS	Sodium dodecyl sulphate
SPSS	Statistical package for the social sciences

S-type	Syringyl type
TAE	Tris-Acetate-EDTA
Tm	Melting temperature
U	Unit
Mg	Microgram
µl	Microliter
UPM	Universal primer A mix
UPM	University Putra Malaysia
USR	Upper stem rot
UTR	Untranslated region
UV	Ultraviolet
Vol	Volume
VP	Versatile peroxidase
wpi	Week post-inoculation
w/v	Weight per volume
X-gal	5-bromo-4-chloro-3-indolyl-β-D-galactopyranoside

CHAPTER 1

INTRODUCTION

Agriculture is an important sector to the sustenance of daily life and economic system of a country. Being an efficient oil crop, oil palm (*Elaeis guineensis* Jacq.), a tropical perennial tree has been planted in many countries including Malaysia. Oil palm was first brought to Malaya by British in 1870s as an ornamental plant which then turned into a commercial plant in the agriculture sector. Palm oil has gained the fastest growing demand globally because it serves as an ingredient in many products including food, cosmetic and bioenergy (Ferdous Alam *et al*., 2015). In Malaysia, the latest oil palm land coverage has reached 5.84 million hectares in 2018 giving rise to 17.16 tonnes/hectare of fresh fruit bunch (FFB) and 3.42 tonnes/hectare of palm oil (Malaysian Palm Oil Board, 2019a; Malaysian Palm Oil Board, 2019b; Malaysian Palm Oil Board, 2019c). Palm oil production is threatened by stem rot caused by *Ganoderma boninense*, leading to major yield loss (Tisné *et al*., 2017).

Ganoderma boninense is a deadly white-rot basidiomycete which inflicts death to oil palm trees. White-rot basidiomycetes fully digest lignin while leaving behind white cellulose (Paterson, 2007). The major disease caused by *G. boninense* is Basal Stem Rot (BSR), a common recurrent disease in oil palm plantations (Ariffin *et al*., 2000) when oil palm trees are replanted. The disease progresses slowly without obvious symptoms during initial stage. Fruiting body appeared at a later stage of infection whereby the transportation of water and nutrient supply are greatly destructed (Ahmadi *et al*., 2017). Successful penetration of pathogenic fungi through cuticle and cell wall into host cells is the key to pathogenicity (An *et al*., 2018). Cell wall degrading enzymes (CWDEs) are needed by plant pathogenic fungi to penetrate plant cell wall (Kubicek *et al*., 2014).

Lignin degrading enzymes (LDEs) are a subset of CWDEs specialize in depolymerisation of lignin. LDEs include LiP, MnP and Lac. Ho *et al*. (2016) found that LDE genes for MnPs and Lacs were up-regulated when oil palm was infected. There are many factors that can affect LDE secretion such as ratio of carbon to nitrogen, pH, temperature and mediators (Asgher *et al*., 2016b). The production of LDEs from white-rot basidiomycetes was found to be suppressed upon application of nitrogen fertilizer (Magill and Aber, 1998).

Soil fertility is important in ensuring plant biomass production. The macronutrients of soil are nitrogen, phosphorus and potassium (Emamgholizadeh *et al*., 2017). Over time, soil fertility declines with continuous cropping. This often resulted in increased usage of fertilizers to restore soil fertility and supply nutrients for plant growth. Insufficient nitrogen in plants increases susceptibility of plants to pathogens (Snoeijers *et al.*, 2000). In addition, the forms of nitrogen (ammonium or nitrate) also affect pathogenesis (Huber and Watson, 1974). In the case of tobacco, nitrate induces resistance and ammonium compromises resistance host plant against hemibiotrophic pathogen (Gupta *et al*., 2013).

Other than nutrient availability, phytohormones also affect pathogenicity (Ma and Ma, 2016). Salicylic acid (SA) is a phenolic compound produced by plants, and its biosynthesis and signaling pathway have been well characterized, demonstrating its important role as a signal involved in the plant defense against biotrophic pathogens (De Coninck *et al*., 2015). Jasmonic acid (JA) is a signalling molecule in plant defense against necrotrophic pathogens (De Coninck *et al*., 2015). *Ganoderma boninense* is a hemibiotroph, having both biotrophic and necrotrophic lifestyles. Thus, SA and JA may affect the pathogenicity of *G. boninense*. It was found that SA affects the secretion and enzyme activities of LDEs of *G. boninense* (Surendran *et al*., 2018). Surendran *et al*. (2018) also stated that phenolic compounds can be inhibitors for LDEs. However, literatures on the effect of SA and JA on gene expression for LDEs in *G. boninense* are not available.

To date, there is no efficient ways for BSR management despite many approaches have been taken (Ahmadi *et al*., 2017). Studies on the effect of different nitrogen sources and phytohormones on the gene expression of LDEs might provide insights into the relationship between oil palm and *G. boninense* during infection. It is hoped that this information can help to lessen the severity of the oil palm disease in the future. This could be achieved by applying suitable nitrogen sources for growth of oil palm while limiting the oil palm disease.

The specific objectives of this study were:

1. To clone transcripts encoding fungal lignin degrading enzymes (LDEs) from *G. boninense* PER71;
2. To measure fungal growth and expression of genes for LDEs of *G. boninense* treated with different nitrogen sources, phytohormones and hydrogen peroxide;
3. To measure plant growth and disease symptoms of oil palm seedlings infected with *G. boninense* under treatment of different nitrogen sources.

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