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EFFECTS OF HERBICIDES, HYDROGEN PEROXIDE AND PHYTOHORMONES ON *Ganoderma* INFECTION IN OIL PALM (*Elaeis guineensis* Jacq.) ROOTS

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By

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Basal Stem Rot (BSR) caused by *Ganoderma* is the major disease that infects oil palms (*Elaeis guineensis* Jacq.). Application of herbicides in plantations for weed control might affect BSR development. The effects of hydrogen peroxide (H_2O_2) and phytohormones which are key signalling agents in plant defense mechanisms on *Ganoderma* infection are unknown. Therefore, the objectives of this study are to investigate the effects of herbicides, H_2O_2 and phytohormones on *Ganoderma* infection in oil palm roots, and to profile the gene expression of transcripts related to hydrogen peroxide production, hormone biosynthesis and signaling during *Ganoderma* infection in oil palm roots. The effects of three commonly used herbicides in plantations on the growth of *Ganoderma* spp. and infection progress in *G. boninense* PER71-inoculated oil palm seedlings were examined. Evaluation on the tolerance of *G. boninense* (pathogenic), *G. miniatocinctum* (pathogenic), and *G. lucidum* (non-pathogenic) to herbicides revealed that glyphosate (Roundup®, GLY) 1800 ppm-2700 ppm can reduce the growth of all three *Ganoderma* species. Both Basta (GLA at 750-3000 ppm) and Paraquat (PQ at 325-300 ppm) inhibited the growth of all three *Ganoderma* species studied except for *G. lucidum* which was able to grow at 650 ppm PQ. GLA and PQ increased the disease severity of oil palm to *Ganoderma* infection. The fungus may avoid the herbicide contaminated soil environment and then infected the oil palm seedlings that could have been weakened by the herbicides. The open reading frame and conserved functional domains of eight cDNAs encoding H_2O_2, phytohormone biosynthesis and signalling in oil palm were analyzed. The transcript abundance of *EgRBOHB2* in *G. boninense*-treated oil palm roots increased 2.42 fold at 3 wpi compared to uninoculated oil palm seedlings. Meanwhile, *EgRBOHB1*, *EgRBOHH* and *EgHIR* did not show significant changes in expression at all three time points. The transcript abundance of EgCOI (jasmonic acid, JA-related) increased at 6 and 12 wpi whereas the transcript abundance EgNPR1 (salicyclic acid, SA-related)

increased at 3 wpi, reduced at 6 and 12 wpi; suggesting a well-coordinated signal crosstalk between JA and SA. The expression of EgOPR which is related to JA biosynthesis was up-regulated at 6 wpi; coincided with the upregulation of EgCOI (which perceives JA). The EgACO1 (ethylene, ET- related) was also upregulated at the early stage of infection by 3.2 and 2.2 fold at 3 and 6 wpi in the inoculated oil palm seedlings, respectively. The exogenous application of phytohormones did not suppress the BSR in *Ganoderma*-inoculated oil palm seedlings while the application of their inhibitors, caused an early onset and more severe disease symptoms. DPI pre-treatment was the only treatment that delayed the onset and reduced the severity of disease symptoms. The distilled water-treated *Ganoderma* inoculated oil palm fresh root samples (control) had a significantly higher H_2O_2 level at 3 wpi compared with uninoculated oil palm root samples. However, there was no significant difference in H_2O_2 level between the *Ganoderma* inoculated and uninoculated oil palm root sample of the other phytohormone-treated or their inhibitor treated oil palm seedlings. The JA-treated and *Ganoderma*-inoculated oil palm root sample had the lowest H_2O_2 level among all the other roots samples at 6 wpi while the SA-treated, *Ganoderma* inoculated oil palm roots had the lowest H_2O_2 level among all the other root samples at 12 wpi. The H_2O_2 inhibitor- treated oil palm roots generally had lower H_2O_2 level when compared with other treatments. Overall, the H_2O_2 levels did not correspond to the disease symptoms and severity but showed an increase at the onset of disease symptoms. In conclusion, the findings from this study have given an insight on the effects of herbicides, H_2O_2, phytohormones and their inhibitors on *Ganoderma* infection and disease progress of BSR in oil palm seedlings.

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sebagai memenuhi keperluan untuk ijazah Master Sains

KESAN RACUN RUMPAI, HIDROGEN PEROKSIDA DAN HORMON TUMBUHAN KE ATAS INFEKSI *Ganoderma* PADA AKAR ANAK BENIH KELAPA SAWIT (*Elaeis guineensis* Jacq.)

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Reput pangkal batang (BSR) yang disebabkan oleh kulat patogenik, *Ganoderma* adalah penyakit utama yang menjangkit kelapa sawit (*Elaeis guineensis* Jacq.). Penggunaan racun rumpai di ladang kelapa sawit untuk pengawalan rumpai mungkin mempengaruhi perkembangan BSR. Kesan hidrogen peroksida (H_2O_2) dan hormon tumbuhan yang merupakan ejen pengisyaratan utama dalam mekanisme pertahanan tumbuhan ketika jangkitan *Ganoderma* tidak diketahui. Oleh itu, objektif kajian ini adalah untuk mengkaji kesan racun rumpai, H_2O_2 dan hormon tumbuhan ke atas jangkitan *Ganoderma* pada akar kelapa sawit, dan untuk memprofil ekspresi gen yang berkaitan dengan penghasilan hidrogen peroksida, biosintesis hormon dan pengisyaratan sistem pertahanan semasa jangkitan *Ganoderma* pada akar benih kelapa sawit. Kesan tiga racun rumpai yang biasa digunakan untuk mengawal pertumbuhan rumpai ke atas pertumbuhan *Ganoderma* spp. dan jangkitan *G. boninense* PER71 pada benih kelapa sawit telah diselidik. Pemeriksaan toleransi *G. boninense* (patogenik), *G. miniatocinctum* (patogenik), dan *G. lucidum* (tidak patogenik) kepada racun rumpai mendedahkan bahawa ® (GLY) pada kadar 1800-2700 ppm merencat pertumbuhan ketiga-tiga species *Ganoderma*. Basta (GLA, 750-3000 ppm) dan Paraquat (PQ, 325-1300 ppm) menyekat pertumbuhan ketiga-tiga spesis *Ganoderma* kecuali *G. lucidum* yang dapat tumbuh di atas media mengandungi 650 ppm PQ. GLA dan PQ mengakibatkan jangkitan *Ganoderma* yang paling serius pada akar kelapa sawit. Fungus tersubut mungkin terpaksa mengelak dari tanah yang dicemari racun rumpai lalu menjangkiti benih kelapa sawit yang mungkin telah dilemahkan oleh racun rumpai. Domain fungsian dan motif terpelihara lapan cDNA terpilih yang berkaitan dengan H_2O_2, biosintesis hormon tumbuhan dan pengisyaratan pertahanan dalam kelapa sawit telah dianalisis. Aras transkrip EgRBOHB2 daripada akar kelapa sawit yang diinokulasi *G. boninense* meningkat 2.42 kali pada 3 minggu selepas inokulasi

(wpi) berbanding kelapa sawit yang tidak diinokulasi. Manakala, ekspresi gen EgRBOHB1, EgRBOHH dan EgHIR tidak menunjukkan perubahan signifikan pada tiga titik masa yang dikaji. Tahap transkrip EgCOI (berkait dengan asid jasmonik, JA) meningkat pada 6 wpi dan 12 wpi manakala, tahap transkrip EgNPR1 (berkait dengan asid salisiklik, SA) meningkat pada 3 wpi, berkurang pada 6 dan 12; wpi menunjukkan penyelarasan isyarat hormon JA dan SA yang baik. Ekspresi EgOPR yang berkaitan dengan biosintesis JA meningkat pada 6 wpi selaras dengan peningkatan ekspresi EgCOI yang mentafsir isyarat JA. Ekpresi EgACO1 (biosintesis etilena, ET) juga meningkat secara signifikan sebanyak 3.2 dan 2.2 kali ganda pada 3 dan 6 wpi pada kelapa sawit yang telah diinokulasikan. Aplikasi hormon tumbuhan tidak membataskan BSR pada benih kelapa sawit manakala aplikasi perencat hormone telah menyebabkan permulaan simptom infeksi yang awal dan kesan penyakit yang paling serius. Hanya rawatan dengan perencat H_2O_2 memperlambatkan simptom penyakit reput pangkal batang. Benih kelapa sawit yang dirawat dengan air-suling dan diinokulasi dengan *Ganoderma* mempunyai tahap H_2O_2 yang lebih tinggi berbanding dengan benih yang tidak diinokulasi. Sampel akar kelapa sawit yang dirawat dengan JA dan diinokulasi *Ganoderma* mempunyai tahap H_2O_2 paling rendah pada 6 wpi, manakala kelapa sawit yang dirawat dengan SA dan diinokulasi *Ganoderma* mempunyai tahap H_2O_2 paling rendah pada 12 wpi. Akar benih kelapa sawit yang dirawat dengan perencat H_2O_2 menunjukkan tahap H_2O_2 yang rendah berbanding dengan rawatan lain. Pada keseluruhannya, tahap H_2O_2 tidak menunjukkan perkaitan dengan symptom penyakit tetapi menunjukkan peningkatan pada permulaan symptom penyakit. Kesimpulannya, penemuan kajian ini telah memberi pengetahuan mengenai kesan racun rumpai, H_2O_2, hormon tumbuhan dan perencat hormon ke atas jangkitan *Ganoderma* dan perkembangan penyakit BSR pada kelapa sawit.

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

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LIST OF ABBREVIATIONS

°C	Degree celsius
%	Percentage
A260nm	Optical density at wavelength 260 nanometer
µg	Microgram
µL	Microliter
µM	Micromoles
BLAST	Basic local alignment search tool
bp	Base pair
BSR	Basal Stem Rot
C:I	Chloroform : Isoamylalcohol
CaCl2	Calcium chloride
cDNA	Complementary deoxyribonucleic acid
cm	Centimetre
Ct	Threshold cycle
CTAB	Cetyltrimethylammonium Bromide
CWDE	Cell wall degrading enzyme
DAMP	Damage associated molecular protein
DEPC	Diethylpyrocarbonate
DNA	Deoxyribonucleic acid
DNase	Deoxyribonuclease I
dNTP	deoxynucleoside triphosphate
EDTA	Ethylenediaminetetraacetic acid
E	Efficiency
EST	Expressed sequence tag
ET	Ethylene
ETI	Effector-triggered immunity
ETS	Effector-triggered susceptibility
g	Gram
GLA	Glufosinate ammonium
GLY	Glyphosate
H2O2	Hydrogen Peroxide
HR	Hypersensitive response
JA	Jasmonic Acid
K	Potassium
kDA	Kilodaltons
L	Litre
LiCl2	Lithium chloride
M	Molar
mA	MilliAmps
MAMP	Microbe-associated molecular pattern
mg	Miligram
min	Minute
mm	Milimetre
mM	Milimolar
MPOB	Malaysian Palm Oil Board
NADPH	Nicotinamide adenine dinucleotide phosphate
NCBI	National Centre for Biotechnology Information

ng	Nanogram
OD	Optical density
ORF	Open reading frame
PAL	Phenylalanine ammonia lyase
PAMP	Pathogen-associated molecular pattern
PBZ	Paclobutrazol
P:C:I	phenol:chloroform:isoamylalcohol
PCR	Polymerase chain reaction
PDA	Potato dextrose agar
qRT	Quantitative reverse transcription
RNA	Ribosome inactivating protein
rpm	Revolutions per minute
RT	Reverse transcriptase
s	second
SA	Salicylic acid
SAR	Systemic acquired resistance
SDS	Sodium dodecyl sulphate
TAE	Tris-acetate-EDTA
U	Unit
UV	Ultraviolet
v/v	volume/volume
w/v	weight/volume
wpi	week post inoculation
× g	times gravity
UPM	Universiti Putra Malaysia

CHAPTER 1

INTRODUCTION

1.1 Introduction

Oil palm (*Elaeis guineensis* Jacq.) is the major agricultural crop grown in Malaysia with 5.81 million hectares of land used for cultivation nationwide (MPOB, 2017). Despite all the efforts to increase the yield of palm oil to meet the increasing demand, basal stem rot (BSR) caused by *Ganoderma* sp. (Hasan *et al*., 2005) still remains as the major devastating disease that reduces not only the productivity but also the normal economic life span of the palm. Successive replanting on the same land after removing the previously BSR infected stands has increased the disease incidence of BSR as the infective tissues, inoculums and spores of *Ganoderma* spp. still remain at the sites (Turner, 1981; Ariffin *et al*., 2000). Besides that, *Ganoderma* spp. have shown the ability to adapt to various environment and food sources (Wong *et al.*, 2012) turning this notorious disease a nightmare to the planters. To date, no effective treatment has been reported to be able to curb this disease.

Herbicides are inevitable inputs to control weeds in oil palm plantations. Although herbicides are effective in controlling weed population, administration of these synthetic chemicals may alter the soil microbial community causing potential increase of opportunistic plant pathogens. Moreover, herbicides may also have non-targeted effects on the cultivated crops making them more susceptible to diseases (Johal and Huber, 2009). Previous studies showed that white rot fungi are more tolerant to herbicides as they produce lignin degrading enzymes that are highly oxidative, non-specific and are able to transform a wide range of herbicides (Kersten and Cullen, 2007; Asgher et al*.*, 2008; Moreira et al., 2013). Besides that, this group of fungi can grow on agricultural waste substrates. However, the influence of the herbicide usage on soil microbial ecosystem and interactions of oil palm and pathogenic white rot fungi such as *Ganoderma* in modulating disease development is rarely reported.

Plants naturally activate their defense mechanism in response to biotic and abiotic stresses. Hydrogen peroxide (H_2O_2) and other reactive oxygen species (ROS) are the key components of plant defense response (Bhattacharjee, 2012). This rapid accumulation of H_2O_2 or also known as 'oxidative burst' caused by environmental or developmental stresses (abiotic, biotic or physiological) regulates a specific subset of transcription factors that initiate changes in gene expression resulting in activation of various mechanisms including plant defense (Desikan *et al*., 2000; Neill *et al*., 2001). Plant immunity is dependent on the interaction between H_2O_2 and other components such as nitric oxide and plant phytohormones as oxidative burst alone is not sufficient to trigger defense pathways (Delledonne *et al*., 2001).

Previous studies have shown that phytohormones mainly salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) contribute in plant defense through the ROS production triggered by pathogen-associated molecular patterns (PAMPs) and effectors (Kunkel and Brooks, 2002; Mur *et al*., 2006; Pieterse *et al*., 2009; Janda, 2015). Although phytohormones play a key role in plant defense mechanism, their roles during various plant-pathogen interaction especially oil palm-*Ganoderma* interaction remains widely uncharacterized (van Loon *et al*., 2006).

BSR caused by *Ganoderma* has been studied for decades since its first detection. However, the interaction between oil palm and pathogen, *Ganoderma* is still not well understood or characterized. In recent years, the availability of oil palm genome sequence, gene expression analysis using expressed sequence tags (ESTs), and studies on differentially expressed genes (DEGs) in *Ganoderma*-inoculated root tissues have provided insights on the expression of defense related genes. Various pathogenesis and defense related genes such as chitinases, glucanases, isoflavone reductase, metallothioneins, metallothionein-like protein, early methionine-labelled polypeptides, type 2 ribosome inactivating proteins, Bowman Birk serine protease inhibitor, cysteine and nitric oxide associated 1 protein have been reported to be differentially expressed in *Ganoderma*-inoculated oil palm root tissues (Naher *et al*., 2011, Yeoh *et al*., 2012; Tan *et al*., 2013; Tee *et al*., 2013, Kwan *et al*., 2015). Genes encoding signal perception and transduction, phytohormone biosynthesis and signalling, ROS biosynthesis and scavenging, transcription factor, secondary metabolite production, and many others that are involved in defense responses were also reported among the DEGs of *Ganoderma*-inoculated oil palm roots in comparison with the uninoculated roots (Ho *et al*., 2016). These up and down-regulated DEGs could either be involved in the oil palm defense mechanism against *Ganoderma* invasion or a result of host defense suppression caused by the fungal pathogen.

In this study, the effects of herbicides, phytohormones and their inhibitors were monitored in infected oil palm roots by recording the morphological changes and disease severity. The expression of genes related to oxidative burst, SA and JA biosynthesis and signaling were profiled using *Ganoderma*-infected oil palm root samples to investigate the involvement of H_2O_2 and phytohormones during defense response of oil palm seedlings against *Ganoderma boninense* at 3, 6 and 12 week post inoculation (wpi). Analyzing the expression of genes involved during the initial stage of infection such as genes encoding hypersensitive-induced reaction (HIR) protein, proteins related to oxidative burst, phytohormone biosynthesis and signaling proteins following the pathogen challenge may provide information on the role of H_2O_2 and phytohormones during oil palm *Ganoderma* interaction.

1.2 Objectives of study

1. To investigate the effects of herbicides, phytohormones and their inhibitors on basal stem rot disease progression in oil palm roots;
2. To profile the expression of transcripts related to hydrogen peroxide production, hydrogen peroxide-induced cell death, hormone biosynthesis and signaling in Ganoderma infected oil palm roots.

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