IDENTIFICATION, CHARACTERISATION AND FUNCTIONAL ANALYSIS OF ELICITOR PROTEINS FROM *Ganoderma boninense*

By

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

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Chair : Professor Wong Mui Yun, PhD
Institute : Tropical Agriculture and Food Security

Ganoderma boninense, the causal agent of Basal Stem Rot (BSR) disease, threatens oil palm production in Southeast Asia where there is no effective control method currently available. The fungus, like various phytopathogenic fungi, is anticipated to secrete elicitor proteins that modify plant immune responses to promote infection during its early interaction with oil palm. Understanding the roles of *G. boninense* elicitor proteins in oil palm root penetration and pathogenicity is imperative for developing effective BSR disease management strategies. Therefore, this study focused on (i) the isolation and identification of candidate elicitor proteins with hypersensitive response (HR)-inducing activity from the culture filtrate of *G. boninense,* (ii) the isolation, characterisation and expression analysis of genes encoding two cerato-platanin proteins in *G. boninense*-oil palm pathosystem, and (iii) the elucidation of the elicitation of early defence responses and the improvement of disease resistance by extracellular protein sample from *G. boninense* in oil palm. In this study, peptide matches to candidate elicitor proteins such as cellulases, chitinase, glucanases, pectate lyases, xylanases, cerato-platanin (CP) proteins, fungalysin and carboxypeptidases were identified in two active fractions obtained from a bioassay-guided fractionation of the 14-day-old fungal culture filtrate using anion exchange chromatography (AIEX), followed by a nano-LC-MS/MS analysis of the active AIEX fractions against the UniProtKB database of *G. sinense* ZZ0214-1. GbCP2 and GbCP6 were identified as potential elicitor proteins based on their effector properties in a bioinformatic investigation of GbCP1 through 9, the *G. boninense* CP gene models. The coding regions of 528 bp and 450 bp of *GbCP2* and *GbCP6*, respectively, were successfully isolated using polymerase chain reaction (PCR) method. The deduced amino acid sequences of GbCP2 and GbCP6 resembled elicitor CP proteins from several ascomycetes and basidiomycetes. The quantitative real-time PCR analysis of *GbCP2* and *GbCP6* in oil palm root-infecting mycelia at 3, 7 and 11 d after inoculation (DAI) revealed that *GbCP6* was significantly up-regulated by 16.3-fold at 11 DAI. GbCP2, on the other hand, was not

differentially expressed at any sampling point, indicating that the protein may have a different function. Besides, the extracellular protein sample induced HR-associated cell death and reactive oxygen species (ROS) generation in oil palm leaf sections at 24-h post-infiltration. In addition, the activities of guaiacol peroxidase and superoxide dismutase enzymes were significantly higher in extracellular protein sample-treated oil palm roots at 12, 24, 48, and 72 h post-treatment (hpt) compared to the control. Significant induction of *RbohB*, a gene encoding respiratory burst oxidase homolog B, by 2.5-fold at 12 hpt further confirmed ROS accumulation and the HR-inducing potential of the extracellular protein sample. BSR disease incidence of 45% and disease reduction of 71.43% at 9 months after inoculation showed the potential of the extracellular protein sample from *G. boninense* strain PER71 as a plant defence activator. In light of all findings, it can be concluded that *G. boninense* secretes elicitor proteins that elicit events involved in early defence during *G. boninense*-oil palm interaction.

Keywords: basal stem rot, elicitor proteins, *Ganoderma boninense* hypersensitive response, oil palm

SDG: GOAL 12: Responsible Consumption and Production

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PENGENALPASTIAN, PENCIRIAN DAN ANALISIS FUNGSI PROTEIN-PROTEIN PENGELISIT DARIPADA *Ganoderma boninense*

Oleh

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Ganoderma boninense, agen penyebab penyakit reput pangkal batang, mengancam pengeluaran kelapa sawit terutamanya di Asia Tenggara di mana tiada kaedah kawalan berkesan tersedia setakat ini. Kulat ini, seperti pelbagai kulat fitopatogen, dijangka merembeskan protein pengelisit yang mengubah suai tindak balas imun tumbuhan untuk menggalakkan jangkitan semasa interaksi awal dengan kelapa sawit. Memahami peranan protein pengelisit *G. boninense* dalam penembusan akar sawit dan kepatogenan adalah penting untuk membangunkan strategi pengurusan penyakit reput pangkal batang yang berkesan. Oleh itu, kajian ini tertumpu kepada (i) pengasingan dan pengenalpastian calon protein pengelisit dengan aktiviti rangsangan seperti tindak balas hipersensitif (HR) daripada tapisan kultur *G. boninense*, (ii) pengasingan, pencirian dan analisis ekspresi gen yang mengekodkan dua protein cerato-platanin (CP) dalam patosistem *G. boninense*- sawit, dan (iii) penjelasan tentang rangsangan tindak balas pertahanan awal dan peningkatan rintangan penyakit oleh sampel protein daripada G*. boninense* pada sawit. Dalam kajian ini, peptida sepadan dengan calon protein pengelisit seperti selulase, kitinase, glukanase, pektat liase, xilanase, protein CP, fungalisin dan karboksipeptidase telah dikenal pasti dalam dua pecahan aktif yang diperoleh daripada pemisahan berpandukan biocerakin bagi tapisan kultur kulat yang berumur 14 hari menggunakan kromatografi pertukaran anion (AIEX), diikuti dengan analisis nano-LC-MS/MS bagi pecahan AIEX aktif terhadap pangkalan data UniProtKB *G. sinense* ZZ0214-1. GbCP2 dan GbCP6 dikenal pasti sebagai protein pengelisit yang berpotensi berdasarkan sifat efektor mereka dalam penyiasatan bioinformatik GbCP1 hingga 9, model gen *G. boninense* CP. Seksyen pengekodan 528 bp dan 450 bp bagi GbCP2 dan GbCP6, masing-masing, telah berjaya diasingkan menggunakan kaedah tindak balas

rantai polimerase. Jujukan asid amino GbCP2 dan GbCP6 yang disimpulkan menyerupai protein pengelisit CP elicitor daripada beberapa askomiset dan basidiomiset. Analisis kuantitatif tindak balas berantai polimerase masa nyata GbCP2 dan GbCP6 dalam miselia yang menjangkiti akar sawit pada 3, 7, dan 11 hari selepas inokulasi (DAI) mendedahkan bahawa *GbCP6* dikawal secara bererti sebanyak 16.3 kali ganda pada 11 DAI. *GbCP2*, sebaliknya, tidak diekspresikan secara berbeza pada mana-mana titik pensampelan, menunjukkan bahawa protein ini mungkin mempunyai fungsi yang berbeza. Selain itu, sampel protein ekstraselular menyebabkan kematian sel serupa HR dan penjanaan spesies oksigen reaktif (ROS) dalam daun sawit pada 24 jam selepas suntikan. Di samping itu, aktiviti enzim guaiacol peroksidase dan superoksida dismutase adalah tinggi secara bererti dalam akar sawit yang dirawat dengan sampel protein ekstraselular pada 12, 24, 48 dan 72 jam selepas rawatan (hpt) berbanding kawalan. Induksi bererti *RbohB*, gen pengekodan letusan respirasi oksidase homolog B, sebanyak 2.5 kali ganda pada 12 hpt seterusnya mengesahkan pengumpulan ROS dan potensi rangsangan HR bagi sampel protein ekstraselular. Insiden penyakit reput pangkal batang sebanyak 45% dan pengurangan penyakit sebanyak 71.43% pada 9 bulan selepas inokulasi menunjukkan potensi sampel protein ekstraselular daripada *G. boninense* strain PER71 sebagai pengaktif pertahanan tumbuhan. Berdasarkan semua penemuan, dapat disimpulkan bahawa *G. boninense* merembeskan protein pengelisit yang mencetuskan kejadian yang terlibat dalam pertahanan awal semasa interaksi antara *G. boninense* dan sawit.

Kata kunci: *Ganoderma boninense*, protein pengelisit, reput pangkal batang, sawit, tindak balas hipersensitif

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AIEX	Anion Exchange Chromatography
ANOVA	Analysis of variance
APX	Ascorbate peroxidase
AUDPC	Area under the disease progress curve
Avr	Avirulence
bp	Base pair
BCAs	Biocontrol agents
BLAST	Basic Local Alignment Search Tool
BSA	Bovine serum albumin
BSR	Basal stem rot
Ca^{2+}	Calcium ion
CAP	Cysteine-rich secretory protein, antigen 5, and pathogenesis-related 1
CAT	Catalase
CBM	Carbohydrate binding domain
cDNA	Complimentary DNA
CP	Cerato-platanin
Cq	Quantification cycle
CWDEs	Cell wall-degrading enzymes
DAB	3′–3′ diaminobenzidine
DAI	Days after inoculation
DI	Disease incidence
DPD	Dip, place and drench

eef2	Elongation factor 2
EIX	Ethylene-inducing xylanase
endoPGs	Endopolygalacturonases
ETI	Effector-triggered immunity
ETS	Effector-triggered susceptibility
GbCP	*G. boninense* Cerato-platanin
gDNA	Genomic DNA
GHs	Glycoside hydrolases
GlcNAc	N-acetyl-D-glucosamine
GPx	Guaiacol peroxidase
GRAVY	Grand average of hydropathy
H_2O_2	Hydrogen peroxide
HIR	Hypersensitive-induced response
HPLC	High performance liquid chromatography
hpt	Hours post-treatment
HR	Hypersensitive response
HSTs	Host-specific toxins
ISR	Induced systemic resistance
ITS	Internal transcribed spacer
LC-MS/MS	Liquid chromatographic separation and mass spectrometry
LC-QTOF-MS/MS	Qualitative tandem liquid chromatography quadrupole time-of-flight mass spectrometry
MAI	Months after inoculation
MALDI-TOF MS	Matrix-assisted laser desorption ionisation with time-of-flight mass spectrometry

MAMPs	Microbe-associated molecular patterns
MAPKs	Mitogen-activated protein kinases
MEA	Malt Extract Agar
MEB	Malt Extract Broth
MPOB	Malaysian Palm Oil Board
MS	Mass Spectrometry
NAD	Nad(p)h dehydrogenase subunit 5-like
NBT	Nitroblue tetrazolium
NCBI	National Centre for Biotechnology Information
NO	Nitric oxide
NPR1	Non-expresser of pathogenesis-related gene 1
NTC	Non-template control
PAMPs	Pathogen-associated molecular patterns
PCR	Polymerase Chain Reaction
PES	Polyethersulfone
Phyre^2	Protein homology/analogy recognition engine v 2.0
pI	Iso-electrical point
PLs	Pectate lyases
PR	Pathogenesis-related
PR1	Pathogenesis-related Gene 1
PRR	Pattern recognition receptor
PTI	PAMP-triggered immunity
R	Resistance
R^2	Coefficient of determination

Rboh	Respiratory burst oxidase homolog
ROS	Reactive Oxygen Species
RT-qPCR	Real-time Quantitative Polymerase Chain Reaction
SA	Salicylic acid
SAR	Systemic Acquired Resistance
SDS-PAGE	Sodium Dodecyl Sulfate–Polyacrylamide Gel Electrophoresis
SEC	Size Exclusion Chromatography
SOD	Superoxide dismutase
TAE	Tris-Acetate-EDTA
TFF	Tangential flow filtration
USDA	United States Department of Agriculture
%DR	Percentage Disease Reduction
2-DE	Two-dimensional Electrophoresis
3D	Three-dimensional

CHAPTER 1

INTRODUCTION

The African oil palm (*Elaeis guineensis* Jacq.) is a perennial oil crop with high oil productivity. It is native to the tropical forests of West and Central Africa. The crop is now being commercially grown in Africa, Latin America, and Southeast Asia due to increasing global demand for crude palm oil and palm kernel oil that serve as raw materials for food and non-food industries (Murphy, 2018; Murphy et al., 2021).

World palm oil production has nearly doubled over the last twelve years, from 44.5 megatonnes (Mt) in 2008 to 73.8 Mt in 2022. At present, Southeast Asia is the leading palm oil production region, with Indonesia and Malaysia being the major producers of palm oil. These countries supply 86.3% of total palm oil supplies (United States Department of Agriculture [USDA], 2023). Malaysian palm oil production has massively increased from 1.3 Mt in 1975 (Gunstone, 2011) to 19.2 Mt in 2020 (USDA, 2021). With a production of 18.2 Mt in December 2022, the country remains the second largest palm oil producer, behind Indonesia (USDA, 2023). Government-funded efforts in oil palm and palm oil research and production have partly contributed to the country's prominence as one of the top palm oil producers in the world.

However, oil palm plantations in Indonesia and Malaysia are under threat from the deadly basal stem rot (BSR) disease caused by *Ganoderma boninense*, a white-rot basidiomycete. The fungus attacks seedlings, young, and mature oil palms (Rees et al., 2012). However, it is most destructive in 10- to 15-year-old oil palms in the plantations (Turner & Gillbanks, 2003). It infects the palm mostly through the roots and spreads to the stem's base, targeting the vascular bundle. The severely infected palm gradually collapses (Cooper et al., 2011). The BSR disease greatly affects the growth, yield, and sustainability of the palms (Flood et al., 2005). For instance, the disease can reduce fresh fruit bunches by 50-80% and can also kill 80% of palm stands when the palms are halfway through their economic life span if the infection spreads across a plantation (Corley & Tinker, 2016).

In Malaysia, BSR has led to huge losses in total revenue generated by the palm oil sector, notably in the previous 30 years, and the loss is expected to rise as BSR incidences rise (Paterson, 2019). BSR disease management in Malaysian oil palm plantations is crucial for meeting the increasing domestic and global demands for palm oil and palm-oil-based products while maintaining the industry's profitability. Nonetheless, it is rather difficult since current BSR disease management measures such as chemical, cultural, and mechanical practices are ineffective and not satisfactory. Therefore, stimulation and

improvement of the palm's innate immunity against the disease is an alternative solution to BSR disease management.

Induced resistance refers to a phenomenon in which plants exhibit an augmented defence capacity when appropriately stimulated by certain beneficial microbes, chemicals, herbivores, pathogens, pests or physical wounding (van Loon et al., 1998; Gamir et al., 2017). It encompasses systemic acquired resistance (SAR) and induced systemic resistance (ISR) which are effective against an array of pathogens and pests (van Loon et al., 2006). Microbe- or plant-derived compounds that are capable of triggering such responses are called elicitors. In recent years, microbe-derived elicitors have received much attention in plant disease control as alternatives to chemical pesticides. Various microbe-derived elicitors have been widely sought and used in molecular plant-pathogen interaction studies to investigate the molecular mechanisms that connect the initial perception of a pathogen and the activation of plant defence responses (Hamid & Wong, 2017).

Bioactive signals such as pathogen-associated molecular patterns (PAMPs), microbe-associated molecular patterns, and danger-associated molecular patterns can activate host resistance when recognised by specialised plant receptors (Durrant & Dong, 2004). The nature of the elicitors influences the activation of PAMP-triggered immunity (PTI) or effector-triggered immunity (ETI) and their corresponding immune responses. Signalling events such as calcium ion influx, reactive oxygen species (ROS) generation, mitogen-activated protein kinases activation and transcriptional reprogramming are common in both PTI and ETI of plants (Dodds & Rathjen, 2010; Yang et al., 2022). Activation of PTI and/or ETI is vital for the induction of systemic resistance in plants. SAR, which is reliant on the salicylic acid (SA) signalling pathway (Gao et al., 2021), provides long-term and powerful protection against an array of pathogens. It is typically associated with programmed cell death that is confined to the infected area and the accumulation of pathogenesis-related (PR) proteins (Durrant & Dong, 2004).

Fungal-derived elicitors such as cerato-platanin (CP) family proteins, endo-1,4-xylanases, oligosaccharides and pectolytic enzymes are well-studied defence activators in host and non-host plants. Among these, CP family proteins are multifunctional in fungi-host interactions. These proteins were able to promote cell death or necrosis, activate plant defence by inducing expression of defence genes and SA, as well as to loosen celluloses in the cell walls in a range of host and non-host plants (Hamid & Wong, 2017). For instance, the HR- and disease resistance-inducing capability of MoHrip proteins from *M. oryzae* has been documented (Chen et al., 2012; Khan et al., 2016). Furthermore, a glycoprotein from *B. cinerea* designated as BcGs1 has also shown necrosis-inducing activity in tomato and tobacco leaves (Zhang et al., 2015). MoHrip and BcGs1 proteins activated PTI through HR and hydrogen peroxide production in host and non-host plants (Chen et al., 2012; Zhang et al., 2015). It is

hypothesised that *G. boninense*, like various fungal phytopathogens, produces elicitor proteins that activate defence responses in oil palm during its early interaction. However, little is known about the fungal elicitor proteins and their involvement during early *G. boninense*-oil palm interaction.

Understanding the significant roles of elicitor proteins in the oil palm root penetration and pathogenicity of *G. boninense*, especially during its early interactions with oil palm, may provide a potential novel strategy for controlling BSR. Intending to discover an environmentally friendly BSR disease control approach, this research focused on the identification of candidate proteins with elicitor activity from *G. boninense*. The elicitors can be used as plant defence activators and exploited as biofungicides to control BSR. In addition, the identification of elicitors can facilitate the development of nanosensors for early detection of *G. boninense* in oil palms in real time.

A research study was, therefore, carried out with the following objectives:

1. To isolate and identify candidate elicitor proteins with hypersensitive response (HR)-inducing activity from the culture filtrate of *Ganoderma boninense* strain PER71.

2. To isolate, characterise and study the expression of genes encoding two cerato-platanin proteins in *G. boninense* strain PER71-oil palm pathosystem *in vitro*.

3. To elucidate the elicitation of early defence responses and the improvement of disease resistance by extracellular protein sample from *G. boninense* strain PER71 in oil palm.

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