



UNIVERSITI PUTRA MALAYSIA

***PHYSIOLOGICAL AND MOLECULAR EFFECTS OF GIBBERELLIC ACID
AND PACLOBUTRAZOL ON YOUNG CLONAL PALM GROWTH AND
DEVELOPMENT***

CHAI SOOK KEAT

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By

CHAI SOOK KEAT

**Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in
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Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfilment of the requirement for the degree of Doctor of Philosophy

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May 2021

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Gibberellin (GA) and paclobutrazol (PBZ) are both plant hormones for stimulating and retardant of plant growth and development, respectively. The role of both hormones in oil palm growth and development is not thoroughly investigated. Therefore, this study focused on the physiological effects of gibberellic acid (GA₃) or PBZ application on young clonal oil palm and its associated molecular responses. It also involved optimization of a tissue preparation procedure for cryosectioning in future transcriptome profiling of inflorescences. Sucrose treatment with snap freezing of fresh oil palm inflorescences provided cryosections with good cellular morphology and higher RNA yields and quality. On phytohormone application, GA₃ and PBZ treatments were separately conducted on young clonal palms for 56 weeks. The GA₃-treated palms were taller with longer fronds than the control but produced lower biomass. These physiological changes were associated with a higher expression of cell cycle-related genes such as *MYB3R-1*, *E2FB*, *CK1d*, *CDK5RAP3* and *SRO1* and cellulose synthase *CSLC5* (five-fold) and *CCR1* (three-fold) for lignin synthesis. In contrast, PBZ application likely blocked GA biosynthesis by suppressing expression of GA biosynthesis genes *GA20ox* and *GA3ox*. PBZ-treated palms were shorter in height and frond length with lower biomass. Higher expression of the growth suppressor *RCC* and two- to eight-fold lower expression of cytoskeletal motor genes *actin 3* and *kinesin 3*, cellulose synthase *CESA2*, pectin activator *WAK3* and *pectin lyase-like* suggested that PBZ may suppressed cell expansion in leaves by enhancing secondary cell wall rigidity in oil palm. Besides that, lower SPAD values together with two- to five-fold lower expression of chlorophyll synthesis genes *UROD*, *ChlD*, *LIL3*, *PORA* and *CAO* suggested that GA₃ suppressed chlorophyll synthesis in GA₃-treated palms. Conversely, three fold higher *GGR* expression in leaflets of PBZ-treated palms associating with higher SPAD values suggested that accumulated geranylgeranyl pyrophosphate (GGPP) due to suppression of GA synthesis might be channeled towards chlorophyll synthesis. On reproductive development, late flowering in PBZ-treated palms correlated with suppression of floral activator *SOC1* while late flowering GA₃-treated palms displayed elevated expression of flowering repressors *LSD1* (three-

fold) and *GATA21* (two- to five-fold) and reduced expression of the flowering accelerator *COL5* (three-fold). However, sex of inflorescences was not affected by these treatments. In conclusion, GA₃ treatment of oil palm promoted height increment and frond elongation by promoting cell division and elongation but suppressed biomass production. On the contrary, growth retardation following PBZ treatment might be attributed to suppression of cell expansion. Both GA₃ and PBZ treatments appeared to delay flowering but did not affect sex determination in young clonal oil palms.



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**KESAN FISIOLOGI DAN MOLEKUL OLEH ASID GIBERELIK DAN
PACLOBUTRAZOL KE ATAS PERTUMBUHAN AND PERKEMBANGAN
KLON KELAPA SAWIT MUDA**

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Giberelin (GA) dan paclobutrazol (PBZ) adalah pengatur pertumbuhan tanaman yang masing-masing merangsang dan merencat pertumbuhan dan perkembangan tanaman. akan tetapi, peranan kedua-dua hormon dalam pertumbuhan dan perkembangan kelapa sawit tidak disiasat dengan menyeluruh. Oleh itu, kajian ini menumpu pada kesan fisiologi rawatan asid giberelik (GA₃) dan PBZ pada klon kelapa sawit muda dan tindak balas molekul yang berkaitan. Ini juga melibatkan pengoptimuman prosedur penyediaan tisu untuk hirisan krio bagi profil transkripome perbungaan masa depan. Rawatan sukrosa dengan pembekuan bunga minyak sawit segar memberikan hirisan krio dengan morfologi selular yang baik serta hasil dan kualiti RNA yang lebih tinggi. Sementara itu, rawatan GA₃ dan PBZ dijalankan secara berasingan pada klon kelapa sawit muda selama 56 minggu. Kelapa sawit yang dirawat dengan GA₃ adalah lebih tinggi, mempunyai pelepah yang lebih panjang berbanding dengan kawalan tetapi menghasilkan biomas yang lebih rendah. Perubahan fisiologi ini dikaitkan dengan pengekspresan yang lebih tinggi gen berkaitan dengan kitaran sel, *MYB3R-1*, *E2FB*, *CK1d*, *CDK5RAP3* dan *SRO1* serta selulosa synthase *CSLC5* (lima kali ganda) dan *CCR1* (tiga kali ganda) untuk sintesis lignin. Sebaliknya, aplikasi PBZ berkemungkinan membantutkan biosintesis GA dengan menyekat ekspresi gen biosintesis GA *GA20ox* dan *GA3ox*. Kelapa sawit yang dirawat dengan PBZ adalah lebih rendah dengan pelepah pendek serta biomassa yang lebih rendah. Ekspresi penyekatan pertumbuhan *RCC* dua kali ganda lebih tinggi manakala dua hingga lapan kali lebih rendah ekspresi gen motor sitoskeletal *actin 3* dan *kinesin 3*, selulosa synthase *CESA2*, pengaktif pektin *WAK3* dan *pektin lyase-like* menunjukkan bahawa PBZ mungkin menyekat pengembangan sel dalam helaian daun dengan meningkatkan ketegaran dinding sel sekunder di kelapa sawit. Selain itu, nilai SPAD yang lebih rendah berserta dengan dua hingga lima kali ganda lebih rendah ekspresi gen klorofil sintesis *UROD*, *ChlD*, *LIL3*, *PORA* dan *CAO* mencadangkan bahawa GA₃ menindas sintesis klorofil di kelapa sawit yang dirawat dengan GA₃. Sebaliknya, tiga kali ganda lebih tinggi ekspresi *GGR* dalam helaian daun kelapa sawit yang dirawat dengan PBZ berkaitan dengan nilai SPAD yang lebih tinggi mencadangkan bahawa geranylgeranyl

pirofosfat (GGPP) yang terkumpul, berikutan penindasan sintesis GA, mungkin telah dialihkan untuk sintesis klorofil. Pada perkembangan pembiakan, proses pembungaan lewat di kelapa sawit yang dirawat dengan PBZ dikaitkan dengan penindasan pengaktif bunga *SOC1* sementara pembungaan lewat di kelapa sawit yang dirawat dengan GA_3 memaparkan lebih tinggi ekspresi penindas pembungaan *LSD1* (tiga kali ganda) dan *GATA21* (dua hingga lima kali ganda) serta pengurangan ekspresi pemecut pembungaan *COL5* (tiga kali ganda). Walau bagaimanapun, seks pembungaan tidak terjejas oleh kedua-dua rawatan ini. Kesimpulannya, rawatan GA_3 atas kelapa sawit mendorong kenaikan ketinggian dan pemanjangan pelepah dengan menggalak pembahagian dan pemanjangan sel tetapi menindas pengeluaran biomassa. Sebaliknya, perencatan tumbesaran berikutan rawatan PBZ mungkin disebabkan oleh penindasan pengembangan sel. Kedua-dua rawatan GA_3 dan PBZ kelihatan seperti melambatkan pembungaan tetapi tidak mempengaruhi penentuan seks klon kelapa sawit muda.



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This thesis was submitted to the Senate of Universiti Putra Malaysia and has been accepted as fulfilment of the requirements 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 |
| 2ODD | 2-oxoglutarate-dependent dioxygenases |
| ABA | Abscisic acid |
| ACS | 1-aminocyclopropane-1-carboxylate synthase |
| AGP | Arabinogalactans |
| AIR12 | Auxin-Induced in Roots |
| AP | Apetala |
| AP2/EREBP | Apetala 2/Ethylene Responsive Element Binding Proteins |
| APC/C | Anaphase-Promoting Complex/Cyclosome |
| APX | Ascorbate Peroxidase |
| ASK19 | S-phase Kinase Associated Protein 19 |
| BAK1 | Brassinosteroid Insensitive 1-Associated Receptor Kinase 1 |
| BES1 | BR-Insensitive-EMS-Suppressor-1 |
| BIN2 | BR Insensitive 2 |
| BR | Brassinosteroid |
| BRI1 | Brassinosteroid Insensitive 1 |
| BSK | BR-signalling kinases |
| BSU1 | BRI1 Suppressor 1 |
| BT4 | BTB and TAZ domain protein 4 |
| BZR-1 | Brassinazole-Resistant-1 |
| CAO | Chlorophyllide a oxygenase |
| CAT | Catalase |
| CCR1 | Cinnamoyl-CoA reductase 1 |
| CDC | Cell Division Cycle |

| | |
|----------|---|
| CDK5RAP3 | CDK Regulatory Subunit Associated Protein 3 |
| cDNA | Complementary DNA |
| Chk1 | Checkpoint Kinase 1 |
| CHS1 | Chalcone Synthase 1 |
| CK1d | Casein Kinase 1 Isoform Delta |
| CNRQ | Calibrated Normalized Relative Quantity |
| CO | Constans |
| COL | Constans-Like |
| COP | Constitutive Photomorphogenesis Protein |
| CPP | <i>ent</i> -Copalyl-Piphosphate |
| CPS | <i>ent</i> -Copalyl Diphosphate Synthase |
| CSL | Cellulose Synthase Like |
| Ct | Cycle threshold |
| CYP2 | Cyclophilin2 |
| DEF | Deficiens |
| DEGs | Differentially Expressed Genes |
| DNA | Deoxyribonucleic Acid |
| DW | Dry weight |
| E | Amplification efficiency |
| ERF3 | Ethylene-Responsive Transcription Factor 3 |
| ERF6 | Relative of Early Flowering 6 |
| ETO1 | Ethylene Overproducer 1 |
| EXP | Expansin |
| F | Female |
| FDR | False discovery rate |
| FF | Fresh frozen |

| | |
|-----------------|---|
| FFPE | Formalin-Fixed, Paraffin-Embedded |
| FLC | Flowering Locus C |
| FLD | Flowering Locus D |
| FLS1 | Flavanone-3-Hydroxylase |
| FPKM | Fragments per kilobase of transcript per million fragments mapped |
| Fr | FronD |
| FT | Flowering Locus T |
| FUL | Fruitful |
| FW | Fresh weight |
| GA | Gibberellin |
| GA13ox | GA13 oxidase |
| GA20ox | GA20 oxidase |
| GA2ox | GA 2-beta-dioxygenase |
| GA ₃ | Gibberellic acids |
| GA3ox | GA3 beta-dioxygenase |
| GAI | GA Insensitive |
| GAMT | GA Methyl Transferase |
| GAPDH | Glyceraldehyde-3-Phosphate Dehydrogenase |
| GGDP | Geranylgeranyl Diphosphate |
| GH17 | O-Glycosyl Hydrolase family 17 protein |
| GH3.5 | Indole-3-acetic acid-amido Synthetase |
| GID1 | GA Insensitive Dwarf 1 |
| GO | Gene Ontology |
| GOI | Gene of interest |
| GRAS | GAI, RGA, and Scarecrow |

| | |
|--------|---|
| GSEA | Gene Set Enrichment Analysis |
| H | Hermaphrodite |
| HMG | 3-hydroxy-3-methylglutaryl |
| HMGS | HMG-CoA synthase |
| IAA20 | Indoleacetic acid-induced protein 20 |
| IDD | Indeterminate Domain |
| INV1 | Invertase 1 |
| IPP | Isopentenyl diphosphate |
| JA | Jasmonate acid |
| JAZ1 | JA ZIM-domain 1 |
| KA | <i>ent</i> -Kaurenoic Acid |
| KO | <i>ent</i> -Kaurene Oxidase |
| KRP2 | Kip-Related Protein 2 |
| KS | <i>ent</i> -Kaurene Synthase B |
| LCM | Laser Capture Microdissection |
| LFY | Leafy |
| LIL3 | Light-Harvesting-Complex Like protein 3 |
| M | Male |
| MEP | Methylerythritol 4-Phosphate |
| mRNA | Messenger Ribonucleic acid |
| MVA | Mevalonic acid |
| MYB308 | MYB-related protein 308 |
| NAD5 | NADH Dehydrogenase subunit 5-like |
| NCBI | National Center for Biotechnology Information |
| NDX1 | Nudix1 |
| NEF1 | No Exine Formation 1 |

| | |
|----------------|--|
| NFL | No Flowering in Short Day |
| NGS | Next-Generation Sequencing |
| NIP1-1 | NOD26-like Intrinsic protein 1-1 |
| NRT | No reverse transcriptase |
| NTC | No template control |
| OCT | Optimal cutting temperature |
| PBZ | Paclobutrazol |
| PCS | Petiole cross section |
| PD00380 | Predicted 40S Ribosomal Protein S27-2 |
| PD00569 | Manganese Superoxide Dismutase |
| PDCB3 | Plasmodesmata Callose-Binding Protein 3 |
| PIF | Phytochrome Interacting Factor |
| PNP1 | Polyribonucleotide Nucleotidyltransferase 1 |
| PORA | Protochlorophyllide Oxidoreductase A |
| pOP-EA01332 | Predicted protein IFH-1 like |
| POX | Peroxidase |
| Q | Phred quality scores |
| qRT-PCR | Quantitative Real-Time Polymerase Chain Reaction |
| R ² | Correlation coefficient |
| RAV1 | Related to ABA-insensitive 3/Viviparous 1 |
| RCC | Regulator of Chromosome Condensation |
| REF6 | Relative of Early Flowering 6 |
| RGA | Repressor of GA1-3 |
| RGL | RGA-Like |
| RIN | RNA Integrity Number |

| | |
|--------|--|
| RNA | Ribonucleic acid |
| ROS | Reactive Oxygen Species |
| SAM | Shoot apical meristem |
| SBP | Squamosa-Promoter Binding Protein |
| SCF | SKP1-Culin-F-box |
| SCL13 | Scarecrow-like 13 |
| SERK2 | Somatic Embryogenesis Receptor-Like Kinase 2 |
| SIM | Kip-Related Protein 2 |
| SKIP11 | SKP1-Interacting Partner 11 |
| SLR | Slender Rice |
| SOC1 | Suppressor of Constans Overexpression 1 |
| SOD | Superoxide Dismutase |
| SPB | Squamosa Promoter Binding Protein |
| SPL | SPB-Like |
| SPL14 | SBP family protein-like 14 |
| SRO1 | Similar to RCD One 1 |
| SVP | Short Vegetative Phase |
| TP | Time Point |
| TBL | Trichome Birefringence-like |
| TSF | Twin Sister of FT |
| UROD | Uroporphyrinogen Decarboxylase |
| WAK3 | Wall-Associated kinase 3 |
| XET | Xyloglucan Endotransglycosylase |
| XTH | Xyloglucan Hydrolase |
| Z-ISO | 15-cis-zeta-carotene |

CHAPTER 1

GENERAL INTRODUCTION

As the world population continues to expand, vegetable oil consumption will increase tremendously. The edible vegetable oil demand has been predicted to triple from 2009 to 2050 (Gottwald, 2018) whereby global consumption of palm oil will quadruple to 240 million tonnes from 2015 to 2050 (Samat, 2018). Consequently, palm oil has emerged as the most consumed vegetable oil since 2010 with 75.45 million metric tons (MT) or 26.3% of global vegetable oil consumption in 2020/21, after soybean oil (28.6%) and rapeseed oil (13.3%) (www.statista.com/statistics). To fulfil and sustain the high demand of palm oil, tissue culture is a promising technique that is able to improve oil palm's yield and quality. It involves the mass propagation of elite high yielding oil palms on culture media to produce more homogeneous clonal oil palms. However, formation of the abnormal mantled inflorescences and fruits in clonal oil palms is the main stumbling block to large scale clonal production. In normal inflorescence development, the male organ will degenerate at stage 4 of flowering development. On the contrary, mantled female inflorescences display feminization of the male organs as the rudimentary stamen primordia of mantled female inflorescences is converted into pseudocarpels and give rise to supernumerary carpel fruits, which results in oil yield losses (Adam *et al.*, 2005). Felda Global Ventures (FGV), which produced 1 million clonal palms annually for sale at RM28 each (Roowi *et al.*, 2018) suffered an estimated loss of RM0.84 million as the result of 3% tissue culture abnormalities in 2015. Unmethylated *Karma* retrotransposon in *EgDEF1*, an *Apetala 3* homolog, leading to truncated *EgDEF1* in mantled inflorescence is the cause of mantling abnormality (Ong-Abdullah *et al.*, 2015). However, the mantling mechanism of floral abnormality remains elusive. Comparative transcriptome analysis of staminodes isolated from normal and mantled inflorescences at stage 3 of flowering development using laser microdissection (LCM) will shed light on the mantling mechanism.

Gibberellins (GAs) are plant growth regulators that stimulate cell elongation and cell division to promote stem elongation (Thomas *et al.*, 2005). Besides that, GAs also promotes juvenile-adult phase transition, whereby low GA levels in shoot meristems prevent differentiation and maintain meristem activity (Hay *et al.*, 2002). A few studies have shown that GAs produce maleness effect on flowering in watermelon (Zhang *et al.*, 2017a), cucumber (Zhang *et al.*, 2017b), spinach (West and Golenberg, 2018), asparagus (Lazarte and Garrison, 1980) and hemp (Ram and Jaiswal, 1972) but promote female flower in maize (Bommineni and Greyson, 1990). In short, GA has been shown to be involved in flower sex determination but the maleness or femaleness effect varies between plants.

Studies of GA effect in oil palm were mainly focused on inflorescences and fruit development. For example, gibberellin-like activity was detected in phloem sap of emergent male inflorescences (Otusanya and Adebona, 1985) while non-bioactive GAs, GA₁₉ and GA₄₄ were in abundance in pre-anthesis inflorescences (Huntley *et al.*, 2002). Besides that, endogenous gibberellic acid (GA₃) level was found peak in early

phase of fruit ripening (10-14 week after pollination) but reduced as fruit matured and ripened (Yeap *et al.*, 2017). Meanwhile exogenous GA₃ treatment on oil palm showed that application conducted 15 days before harvest could increase fruit bunch weight (Kalidas and Rajasekhar, 2010), while no effect was observed in day 1 to 7 in post-harvest treatment (Sudradjat *et al.*, 2021). Besides that, GA₃ application on inflorescences in anthesis induced parthenocarpic fruits without assisted pollination (Thomas *et al.*, 1973). An earlier study conducted on oil palm seedlings for two years showed that GA₃ treatment favoured the production of male inflorescences in young oil palms (Corley, 1976). The result was inconclusive because no further details were available on how GA₃ exerts the sex determination effect on the seedling palms at the molecular, biochemical and physiological levels. Hence, an investigation into the physiological and molecular effects of exogenous GA₃ and its antagonist, paclobutrazol (PBZ), on oil palm clonal materials may provide clues into the role of this hormone in vegetative and flower development, particularly in sex determination. The hypothesis of this study was that GA₃ and PBZ affect the vegetative and reproductive development of the oil palm. The objectives of this study were:

1. to optimize oil palm inflorescence preparation procedures, i.e. formalin-fixed paraffin embedded and fresh frozen, and staining procedures, i.e. naphthol blue black and toluidine blue, for cryosection and LCM,
2. to determine the physiological effects of GA₃ and PBZ on vegetative growth and reproduction in young clonal oil palms,
3. to profile the gene expression changes using transcriptome sequencing in young clonal oil palms due to the GA₃ and PBZ application.

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