



**METAGENOMIC DECIPHERING OF MICROBIAL COMMUNITY
STRUCTURE, DIVERSITY AND FUNCTIONALITY OF THE SOIL-AND-OIL
PALM SEEDLING SYSTEM ASSOCIATED WITH FERTILIZER
APPLICATION**

By

MOHAMAD KHAIRIL BIN RADZALI

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

July 2023

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Abstract of thesis presented to the Senate of Universiti Putra Malaysia in
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Chair : Assoc. Prof. Wan Zuhainis Saad, PhD
Faculty : Biotechnology and Biomolecular Sciences

In well-run Malaysian oil palm plantations, fertilizer management is the highest field cost factor and is often associated with environmental concerns. While inorganic fertilizer effects on crop microbes like maize, wheat, and soybean are extensively studied, oil palm seedling microbial communities and responses, including root changes, microbial shifts, and nutrient uptake, remain insufficiently understood. This prompted the study to investigate microbial community composition, diversity, and functional attributes of the soil-and-oil palm seedling system (bulk soil, rhizosphere, rhizoplane, endosphere) subjected to NPK fertilization using an amplicon sequencing approach and bioinformatic analyses. The fertilizer application substantially ($p < 0.05$) increased soil physicochemical properties including base saturation, total phosphorus, exchangeable magnesium, and potassium. The inorganic fertilizer also increased significantly ($p < 0.05$) the foliar carbon and potassium content as well as the seedling's dry weight. The taxonomic composition of microorganisms revealed Proteobacteria (44.91%), Ascomycota (37.42%), Cyanobacteria (22.85%), and Glomeromycota (12.56%) predominantly distributed across all samples. Alpha diversity demonstrated that the fertilizer application significantly reduced the bacteria across the soil-and-oil palm seedling system yet increased the fungal richness and diversity in bulk soil and rhizoplane. Moreover, the Principal Coordinate Analysis (PCoA) indicated the fertilizer application influenced the microbial communities mainly in the rhizosphere compared to other niches. However, the unfertilized soil enriched a higher number of discriminatory taxa compared to the fertilized based on linear discriminant analysis effect size (LEfSe) analysis. Apart from the enrichment of fungal pathogenicity due to the fertilizer application, the LEfSe also revealed that the treatment enriched functions related to nutrient cycling and plant growth promotions in the microbial communities. Several phyla members belonging to Proteobacteria, Actinobacteria, Acidobacteria, Ascomycota, and

Basidiomycota were recognized as the network keystones as revealed by the co-occurrence network analysis. Based on canonical correspondence analysis, several environmental factors including pH, foliar total carbon and phosphorus, soil total phosphorus, and plant biomass were identified as the significant ($p < 0.05$) key drivers in determining the composition of the microbial communities. These findings provided insights into the microbial composition and potential functions in unfertilized and fertilized soil. The research reveals that the NPK application improves soil properties and seedling growth. To avoid over-fertilization and environmental harm, careful dosage and timing are crucial. While NPK use shifts microbial diversity towards fungi, a balanced community can be maintained by adding organic fertilizers or compost that support bacterial populations and nutrient supply. The study also emphasizes nutrient cycling and growth promotion through LEfSe analysis, suggesting benefits from specific microbial inoculants. Environmental factors like pH, nutrients, and plant biomass guide fertilizer strategies for optimal nutrient uptake and microbial relationships. For long-term sustainability, an integrated approach using inorganic and organic fertilizers is recommended for enhanced soil health and microbial diversity. This research underscores lasting benefits for soil and ecosystem resilience, beyond short-term gains.

Keywords: Oil palm seedlings, microbiome, NPK fertilization, amplicon sequencing, bioinformatic analyses

SDG: GOAL 2: Zero Hunger, GOAL 12: Responsible Consumption and Production, GOAL 15: Life on Land

Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia
sebagai memenuhi keperluan untuk Ijazah Doktor Falsafah

**PENTAFSIRAN METAGENOMIK STRUKTUR KOMUNITI, KEPELBAGAIAN
DAN FUNGSI MIKROB DIDALAM TANAH DAN SISTEM ANAK BENIH
KELAPA SAWIT BERIKUTAN APLIKASI BAJA**

Oleh

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Dalam ladang kelapa sawit Malaysia yang dikendalikan dengan baik, pengurusan baja merupakan faktor kos lapangan yang paling tinggi dan sering dikaitkan dengan kebimbangan alam sekitar. Walaupun kesan baja bukan organik pada mikrob tanaman seperti jagung, gandum dan kacang soya dikaji secara meluas, komuniti dan tindak balas mikrob anak benih kelapa sawit, termasuk perubahan akar, peralihan mikrob dan pengambilan nutrien, masih tidak difahami dengan secukupnya. Ini mendorong penyiasatan tentang komposisi komuniti mikrob, kepelbagaian dan atribut fungsi di dalam tanah dan sistem anak benih kelapa sawit (tanah pukal, rizosfera, rhizoplan, endosfera) yang tertakluk kepada tanah yang tidak dibaja dan dibaja menggunakan pendekatan metagenomik dan analisis bioinformatik. Penggunaan baja telah meningkatkan ($p < 0.05$) sifat fizikokimia tanah dengan ketara termasuk ketepuan asas, jumlah fosforus, magnesium, dan kalium. Baja bukan organik juga meningkatkan ($p < 0.05$) kandungan karbon dan kalium daun serta berat kering anak benih. Komposisi taksonomi mikrob mendedahkan Proteobacteria (44.91%), Ascomycota (37.42%), Cyanobacteria (22.85%), and Glomeromycota (12.56%) secara dominan di semua sampel. Kepelbagaian alfa menunjukkan bahawa penggunaan baja telah mengurangkan ($p < 0.05$) kepelbagaian bakteria di dalam tanah dan sistem anak benih kelapa sawit dengan ketara namun meningkatkan kekayaan dan kepelbagaian kulat terutamanya di tanah pukal dan rhizoplan. Selain itu, Analisis Koordinat Utama (PCoA) menunjukkan bahawa rawatan mempengaruhi komuniti mikrob terutamanya di rizosfera berbanding bahagian lain. Walau bagaimanapun, tanah yang tidak baja memperkayakan taksa diskriminasi yang lebih tinggi berbanding dengan rawatan pambajaan berdasarkan analisis saiz kesan analisis diskriminasi linear (LEfSe). Selain daripada pengayaan patogenik kulat akibat penggunaan baja, LEfSe juga mendedahkan bahawa rawatan baja memperkayakan fungsi yang berkaitan dengan kitaran nutrien dan promosi pertumbuhan tumbuhan dalam komuniti mikrob. Beberapa filum kepunyaan

Proteobacteria, Actinobacteria, Acidobacteria, Ascomycota, dan Basidiomycota telah dikenal pasti sebagai batu kunci rangkaian yang didedahkan oleh analisis rangkaian kejadian bersama. Berdasarkan analisis korespondensi kanonik, beberapa faktor persekitaran yang penting ($p < 0.05$) termasuk pH, jumlah karbon dan fosforus foliar, jumlah fosforus tanah, dan biojisim tumbuhan telah dikenal pasti sebagai pemacu utama dalam menentukan komposisi komuniti mikrob. Penemuan ini memberikan pandangan tentang komposisi mikrob dan potensi fungsi di bawah rawatan tanah yang tidak dibaja dan tidak dibaja. Penyelidikan mendedahkan bahawa aplikasi NPK meningkatkan sifat tanah dan pertumbuhan anak benih. Untuk mengelakkan pembajaan berlebihan dan kemudaratan alam sekitar, dos yang sesuai adalah penting. Walaupun penggunaan NPK mengalihkan kepelbagaian mikrob ke arah kulat, komuniti yang seimbang boleh dikekalkan dengan menambahkan baja organik atau kompos yang menyokong populasi bakteria dan bekalan nutrien. Kajian itu juga menekankan kitaran nutrien dan promosi pertumbuhan melalui analisis LEfSe, mencadangkan faedah daripada inokulan mikrob tertentu. Faktor persekitaran seperti pH, nutrien dan biojisim tumbuhan membimbing strategi baja untuk pengambilan nutrien yang optimum dan hubungan mikrob. Untuk kemampuan jangka panjang, pendekatan bersepadu menggunakan baja bukan organik dan organik disyorkan untuk meningkatkan kesihatan tanah dan kepelbagaian mikrob. Penyelidikan ini menekankan manfaat yang berkekalan untuk daya tahan tanah dan ekosistem, melangkaui keuntungan jangka pendek.

Kata kunci: Anak benih kelapa sawit, mikrobiom, pembajaan NPK, penjujukan amplikon, analisis bioinformatic

SDG: MATLAMAT 2: Sifar Kelaparan, MATLAMAT 12: Penggunaan dan Pengeluaran Bertanggungjawab, MATLAMAT 15: Kehidupan di Darat

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LIST OF ABBREVIATIONS

16S	16 Svedberg
18S	18 Svedberg
ITS	Internal Transcribed Spacer
AOB	Ammonia-Oxidizing Bacteria
Ha	Hectare
PGPM	Plant Growth-Promoting Microorganism
EM	Effective Microbes
ACC	1-Aminocyclopropane-1-Carboxylate
IAA	Indole-3-Acetic Acid
GA	Gibberellin Acid
NGS	Next-Generation Sequencing
MGAS	Marker Gene Amplicon Sequencing
RDP	Ribosomal Database Project
MG-RAST	Metagenomic Rapid Annotation using Subsystems Technology
UCHIME	USEARCH Chimera Slayer
MOTHUR	MULTiple Treads for Heterogeneous 16S rRNA datasets
BioMaS	Bioinformatic analysis of Metagenomic AmpliconS
QIIME	Quantitative Insights into Microbial Ecology
OTU	Operational Taxonomic Unit
PICRUST	Phylogenetic Investigation of Communities by Reconstruction of Unobserved States
Tax4Fun	Taxonomic Framework for Functional Annotation
FUNGuild	Fungal Ecology Network Guild Database

PCR	Polymerase Chain Reaction
DIAMOND	Discriminative Aligner of Protein sequences using Diagonalization
MEGAN	MEtaGenome Analyzer
ASV	Amplicon Sequence Variant
DADA2	Divisive Amplicon Denoising Algorithm 2
MED	Minimum Entropy Decomposition
USEARCH	URich Sequence Analysis with De-replication
ANOVA	Analysis of Variance
PCoA	Principle Coordinate Analysis
NMDS	Non-Metric Multidimensional Scaling
PCA	Principle Component Analysis
PC	Principle Component
ANOSIM	Analysis of Similarity
PERMANOVA	Permutational Multivariate Analysis of Variance
LEfSe	Linear discriminant analysis Effect Size
KW	Kruskal-Wallis
LDA	Linear Discriminant Analysis
CCA	Canonical Correspondence Analysis
CA	Correspondence Analysis
RDA	Redundancy Analysis
RISDA	Rubber Industry Smallholders Development Authority
EC	Electrical Conductivity
TC	Total Carbon
OC	Organic Carbon
TOC	Total Organic Carbon

TN	Total Nitrogen
C/N	Carbon-to-Nitrogen Ratio
TP	Total Phosphorus
AP	Available Phosphorus
CEC	Cation Exchange Capacity
BS	Base Saturation
DW	Dry Weight
WV ⁻¹	Weight in Volume
EA	Elemental Analyzer
UV-Vis	Ultraviolet-Visible Spectrometer
ICP-EOS	Inductively Coupled Plasma Optical Emission Spectrometry
bp	Base pair
FLASH	Fast Length Adjustment of SHort reads
STAMP	Statistical Analysis of Metagenomic Profile
VIF	Variance Inflation Factor
Kos	KEGG Ortholog Groups
C	Unfertilized
F	Fertilized
LCOs	Lipo-chito-oligosaccharides
AMF	Arbuscular Mycorrhizal Fungi
NaCl	Sodium Chloride
B	Bulk Soil
R	Rhizosphere
P	Rhizoplane
ES	Endosphere

EPS	Exopolysaccharide
ATP	Adenosine Triphosphate
PGPR	Plant Growth-Promoting Rhizobacteria
OM	Organic Matter
RSA	Root System Architecture
BSR	Basal Stem Root
PUFAs	Polyunsaturated Fatty Acids
CMC	Carboxymethylcellulose

CHAPTER 1

INTRODUCTION

1.1 Background

Oil palm (*Elaeis guineensis*) is the most cultivated agricultural crop in Malaysia and has been one of the top economic contributors to the country's economy. As of 2021, the crop is grown on 5.73 million hectares in Malaysia, with Peninsular Malaysia having the most oil palm plantations (2.61 million hectares) and Sarawak having the second-largest area (1.61 million hectares) (MPOB, 2022a). The Malaysian palm oil industry generated an average of RM 108.52 billion in export earnings in 2021, making it the most profitable agricultural crop in Malaysia (MPOB, 2022b).

The demand for palm oil is projected to increase as the world's population grows and it is estimated between 93 and 156 million tonnes of palm oil might be needed by 2050 (Pirker et al., 2016; Murphy et al., 2021). A higher yield can be accomplished through optimized fertilizer usage and strategic production techniques. Chemical fertilizers (also known as mineral, inorganic, or synthetic fertilizers) are inorganic salts that have a high concentration of a macronutrient (nitrogen, N; potassium, K; phosphorous, P). Secondary macronutrients such as calcium, magnesium, and sulfur can also be supplemented to the soil via chemical fertilizers.

Although both inorganic and organic fertilizers play a significant role in enhancing agricultural productivity, inorganic fertilizer use is on the rise with an anticipated total of 190 million tonnes in 2019 (FAO, 2022). The increasing use of fertilizer resulted in negative environmental impacts (Dincă et al., 2022). Only 50-60% of synthetic nitrogen fertilizer supplemented to soil is taken up by crops while the remaining run off into water bodies (groundwater or surface) due to high dissolution properties (Scherer, 2005; Bijay-Singh & Craswell, 2021). Apart from contributing to N₂O emissions in the atmosphere (Chai et al., 2019), the use of fertilizer can also have impacts on microorganisms.

Several studies have also demonstrated that chemical or organic fertilization influenced the structure of soil microbial communities' composition, abundance, and diversity. In acidic subtropical forests, chemical N addition increased the relative abundance of oligotrophic bacteria and favored certain bacterial groups such as Ktedonobacteria and Acidobacteria that are involved in C cycling (Cui et al., 2021). On the contrary, intensive mineral N fertilization reduced diazotrophs which were the key rhizosphere microbes with symbiotic N-fixing interactions in

leguminous plants (Dincă et al., 2022). Zheng et al. (2017) also revealed long-term N fertilization decreased the abundance of P-solubilizing bacteria. Therefore, an in-depth understanding of the influence of fertilizer application on oil palm microbial community structure and their functional attributes in response to soil amendments can be achieved through high-throughput sequencing technologies.

Advances in genome sequencing efficiency have accelerated microbiome research, which has mostly relied on two sequencing-based techniques: amplicon and metagenomic sequencing approaches. Amplicon sequencing typically uses 16S rDNA and internal transcribed spacers (ITSs) as specific marker/target genes for prokaryotes (bacteria and archaea) and eukaryotes (fungi) identification, respectively, whereas shotgun sequencing targets the whole genome and captures the entire breadth of DNA (Liu et al., 2021)

Few previous studies have implemented a next-generation sequencing (NGS) approach to explore the influence of fertilizer application on microbial community structures. A study was conducted on a bacterial population subjected to various treatments (organic, inorganic, no fertilizer) and revealed the highest abundance of endophytes in organic fertilizer treatment followed by no fertilizer and inorganic fertilizer. Moreover, major nutrient cycling pathways related to nitrogen and phosphorus metabolism were predominantly found in organic fertilizer-cultivated crops, hence suggesting sustainable agricultural practices (Fadiji et al., 2020c). A different study found a dominant genus (*Bacillus*), as a potential biofertilizer and biocontrol agent in the rhizosphere of chilli seedlings using an amplicon gene sequencing approach (Passari et al., 2018).

1.2 Problem statement, research questions, and hypotheses

Chemical fertilizers, also known as inorganic fertilizers, are used in oil palm agriculture to improve crop yields and promote healthy plant growth. Apart from the increased cost of fertilizers and labor costs, excessive use of chemical fertilizers can have negative impacts on the environment and soil health. The overuse of chemical fertilizer application has resulted in several environmental concerns, such as soil degradation and pollution. It increases soil density and compactness due to the formation, accumulation, and concentration of mineral salts of chemical fertilizers (Massah & Azadegan, 2016), which can limit the capacity of water and air to permeate the soil and cause poor drainage and poor crop development. Moreover, it can pollute soil and water through leaching, runoff, eutrophication, and soil acidification (Yan et al., 2020; Liu et al., 2021).

The excessive use of inorganic fertilizers can also harm beneficial microorganisms in the soil and its surroundings. It decreases the diversity of microorganisms, as some species may be more sensitive to the effects of inorganic fertilizers than others (Pan et al., 2020). Furthermore, the composition of inorganic fertilizers contains toxic chemicals that are harmful to beneficial microorganisms and, subsequently, reduce their function and impact on the overall soil health (Vishwakarma et al., 2020). The excessive use of inorganic fertilizers can also disrupt nutrient transformation, leading to changes in the microbial network (Yu et al., 2019).

However, the understanding of how microorganisms respond to fertilizer application is also poorly understood. Different microbial populations in soil may respond differently to soil nutrient availability, depending on their metabolic capabilities and other factors. This can make it difficult to predict the overall impact of fertilizer on the microbial community. Therefore, it is imperative to understand the microbial communities in the soil-and-oil palm seedling system and how they are affected by fertilizer management practices. The recent advancements in next-generation sequencing steer the main direction of the current study and provide insights into the impacts of inorganic fertilizer application on microbial abundance, diversity, functions, networks, and the correlation with physicochemical properties.

The research questions were: i) How does the application of inorganic fertilizers affect soil physicochemical properties and foliar nutrient contents? ii) What are the changes in the composition and diversity of microbial communities in soil-and-oil palm seedling systems following the NPK fertilization? iii) Are there any specific microbial taxa and functions that could be enriched following the treatment? iv) How does the treatment impact the microbial keystones and co-occurrence network in the soil-and-oil palm seedling system? v) Can environmental factors such as soil physicochemical properties and foliar nutrient contents drive the abundance of microorganisms in the soil-and-oil palm seedling system?

Taken together, we hypothesized that: i) The use of inorganic fertilizers will increase the availability of essential plant nutrients such as nitrogen, phosphorus, and potassium in the soil and foliar of the seedlings. ii) The application of inorganic fertilizers will reduce bacteria but increase fungal diversity in the soil-and-oil palm seedling system. iii) The fertilizer application will enrich microbial taxa and functions potentially linked to nutrient cycling and plant growth promotion. iv) The use of inorganic fertilizers will reduce bacteria yet increase the fungal network in the the soil-and-oil palm seedling system. v) Soil physicochemical properties and foliar nutrient contents will be the environmental drivers of the abundance of enriched taxa in the soil-and-oil palm seedling system.

1.3 Research objectives

The main objective of this research was to investigate how microbial communities, diversity, functions, networks, and correlations with environmental factors were shaped following the NPK fertilization in the soil-and-oil palm seedling system via the amplicon sequencing approach.

To achieve this, several specific objectives were derived, each using an amplicon sequencing approach to evaluate microbial community composition, diversity, functions, co-occurrence networks, and correlations with physicochemical parameters in the soil-and-oil palm seedling system including bulk soil, rhizosphere, rhizoplane, and endosphere. Each objective was addressed in a separate chapter, allowing for a detailed analysis of the different microbial communities in the soil-and-oil palm seedling system. The specific objectives were as follows:

- i. to evaluate microbial community composition, diversity, functions, co-occurrence network, and correlation with physicochemical parameters following the NPK fertilizer application in the bulk soil via amplicon sequencing;
- ii. to evaluate microbial community composition, diversity, functions, co-occurrence network, and correlation with physicochemical parameters following the NPK fertilizer application in the rhizosphere via amplicon sequencing;
- iii. to evaluate microbial community composition, diversity, functions, co-occurrence network, and correlation with physicochemical parameters following the NPK fertilizer application in the rhizoplane via amplicon sequencing; and
- iv. to evaluate microbial community composition, diversity, functions, co-occurrence network, and correlation with physicochemical parameters following the NPK fertilizer application in the endosphere via amplicon sequencing

1.4 Significance of the study

Numerous implications may be drawn from the research on how plants and microbiomes respond to fertilizer application. Specifically, the study can be used to identify specific microbial groups that have important functions in nutrient cycling, biodegradation of pollutants, plant growth promotion, or disease suppression. This information can be used to develop sustainable agricultural strategies such as frequency and optimum rate of inorganic fertilizer in oil palm seedlings.

1.5 Organization of dissertation

Chapter 1 illustrates a general background of the study, the problem statement, the research objectives, the research questions, the significance of the study, and the organization of the dissertation. Chapter 2 provides a critical examination of the existing research and methods on the topic being studied. This includes an overview of the research topic, previous research, research methods, and limitations of the literature. Chapters 3, 4, 5, and 6 cover the studies of microbial communities the soil-and-oil palm seedling system including bulk soil, rhizosphere, rhizoplane, and endosphere, respectively, via an amplicon sequencing approach. The work resulting from the research is summarized and concluded in Chapter 7. This chapter also includes some of the takeaways and highlights of the research for future work.

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