Community of Soil *Actinobacteria* in PTPN VI Oil Palm Plantation Jambi (Sumatra, Indonesia) Based on Amplicon Sequencing of 16S rRNA Gene

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1. Introduction

Palm oil is one agricultural commodity that significantly contributes to the Indonesian economy. Nearly 70% of oil palm plantations in Indonesia are located at Sumatra Island, and the remaining around 30% are at Kalimantan Island. Increased production of oil palm encourages land expansion for oil palm plantations. Most of the lowland forest on Sumatra Island has been converted to rubber (*Hevea brasiliensis*) and oil palm (*Elaeis guineensis*) plantations (Villamor *et al.* 2014). Deforestation and forest transformation impact bacterial diversity and community composition (Schneider *et al.* 2015).

Soil microbes are organisms that have essential roles in determining soil conditions. Soil microbes also contribute to the availability of nutrients in the soil, playing a significant role in plant growth (Nannipieri *et al.* 2003). Soil bacteria are reported as soil organic matter decomposers. They can also recycle the organic residues to make associations with plant roots that eventually help supply essential nutrients such as nitrogen, phosphorus, and potassium. The potential of soil bacteria such as *Pseudomonas corrugate*, *Azospirillum brasilense*, *Rhizobium* sp., *Bacillus subtilis*, and *Streptomyces nojiriensis* for increased plant growth as well as pest and disease control were reported (Bhattacharyya *et al.* 2016).

One of the microbial groups found in soil and known to have many vital roles is *Actinobacteria*. They belong to Gram-positive Bacteria and are widely distributed in nature, especially in soils (Ludwig *et al.* 2012; Castaneda and Barbosa 2017). *Actinobacteria* also play an essential role in agriculture and plantations ecosystems, among others, secreting secondary metabolites to counteract pathogenic fungi responsible for leaf spot, stem rot, and brown germ

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ABSTRACT

In Sumatra, Indonesia, increased oil palm production encourages land expansion for oil palm plantations. And soil *Actinobacteria* have a potential role in agriculture and plantations ecosystems. The use of fertilizer and herbicide affects soil microbial diversity, including *Actinobacteria*. This research analyzed and investigated the community composition and diversity of *Actinobacteria* in soils of oil palm plantations in Jambi Sumatra. Amplicon-based analysis of the 16S rRNA gene (V3-V4 hypervariable region) was used to amplify actinobacterial full-length 16S sequences. The V3-V4 actinobacterial specific 16S rRNA gene sequencing was done using Next-Generation Sequencing. This study confirmed that actinobacterial specific 16S rRNA gene primer could amplify the 16S rRNA gene. Frankiales dominated the community composition of soilborne *Actinobacteria*. The diversity and community composition of soilborne *Actinobacteria* were not significantly affected by the interaction between fertilization and weed treatments. Furthermore, the use of NPK fertilizer significantly affected the abundance of Kineosporiales, whose abundance increased with the increasing concentration of NPK fertilizer. The interaction between fertilization and weeding treatments in the oil palm plantations has no impact on soil Actinobacteria's community composition and diversity.

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Actinobacteria also have a potential role as plant growth-promoting rhizobacteria (PGPR). PGPR are free-living beneficial bacteria that important for agriculture. The PGPR mechanisms are the production of siderophores, indole acetic acid (IAA), nutrient solubilization, and antagonistic or beneficial synergistic effects (Franco-Correa et al. 2010). Actinobacteria is one of the most effective microbes in terms of siderophores production. Some genera of Actinobacteria, such as Streptomyces and Thermobifida, reported a grand synthesis of siderophores (Dimise et al. 2008).

Furthermore, IAA is a plant growth hormone and an active form of auxins. IAA plays a vital role in plant development through its life cycle. The production of IAA has been widely studied in Actinobacteria. Some genera of Actinobacteria such as Streptomyces sp., Nocardia sp., and Kitasatospora sp. have been reported as IAA producers (Dimkpa et al. 2008; Shrivastava et al. 2008). Moreover, Frankia sp. has been known as nitrogen-fixing Actinobacteria. Frankia sp. play a role in symbiotic interaction with the plant roots called actinorhizal symbiosis (Khan et al. 2007).

Additionally, Actinobacteria also have a potential role as mycorrhiza helper bacteria. The majority of plants are symbiotic with mycorrhiza to increase the growth rate. Streptomyces and Thermobifida improved the mycelium growth of Glomus and Gigaspora. The existence of Streptomyces also has a beneficial effect and a good correlation with the germination of the mycorrhizal spores (Merzaeva and Shirokikh 2006).

Soil Actinobacteria have great potential as plant growth-promoting rhizobacteria. So this research was conducted to explore the diversity of soil Actinobacteria and analyze their relation with soil health. However, not all Actinobacteria can be cultured or grown in the laboratory. A solution to overcome the difficulties and limitations of the cultivation technique is metagenomic approaches. These approaches can be used to analyze the community and diversity of Actinobacteria without culturing process. A technique that can be used in metagenomic approaches is amplicon sequencing.

PT Perkebunan Nusantara (PTPN) VI is a state-owned enterprise in Jambi Province (Sumatra, Indonesia) established since 1996. The company is engaged in oil palm (90%), rubber, and tea processing agro-industry. The PTPN VI Jambi use fertilizers and herbicide on oil palm plantations. The fertilizers used in PTPN VI oil palm plantations are NPK (Nitrogen, Phosphorus, and Potassium) fertilizers, and glyphosate was used as an herbicide. The use of fertilizers and herbicides can affect soil microbial activities. The application of herbicides reduced the population of all the bacteria (Latha and Gopal 2010; Sathiyanavini et al. 2015). Otherwise, the community of soil bacterial compositions was increased after the NPK fertilization treatments (Pan et al. 2014).

The community composition and diversity of soilborne Actinobacteria in soils of oil palm plantation in PTPN VI had not yet been described. So, this study aimed to analyze and investigate the community and diversity of Actinobacteria in the soil of PTPN VI plantation affected by the fertilizers and herbicides application in the soils.

2. Materials and Methods

2.1. Soil Sample Collection

The sampling sites were in PTPN VI oil palm plantation Jambi, Sumatra, Indonesia. Soil sampling was carried out at 4 locations of Oil Palm Management (OM) with four different treatments (core plots OM1, OM2, OM3, and OM4). The four treatments are a combination of different concentrations of NPK fertilizer and the weeding method used in the oil palm plantation system. There are two concentrations of fertilizer used, i.e., 260 N, 50 P, 220 K kg ha⁻¹ year⁻¹ (conventional fertilization, designated “C”) and 136 N, 17 P, 187 K kg ha⁻¹ year⁻¹ (reduced fertilization, designated ”R”). There are two types of weeding treatments, i.e., using herbicides 500 cc ha⁻¹ year⁻¹ (designated “H”) and mechanical weeding (designated “W”).

The four treatments combination of soil conditions, i.e., the soil was fertilized with 260 N, 50 P, 220 Kg ha⁻¹ year⁻¹. It was weeded with glyphosate herbicide 500 cc ha⁻¹ year⁻¹ (named “CH”), the soil was fertilized with 260 N, 50 P, 220 Kg ha⁻¹ year⁻¹ and was weeded mechanically (named “CW”), the soil was fertilized with 136 N, 17 P, 187 Kg ha⁻¹ year⁻¹ and was weeded mechanically (named “RH”), and the soil was fertilized with 136 N, 17 P, 187 Kg ha⁻¹ year⁻¹ and was weeded mechanically (named “RW”). The NPK fertilizer was applied at about 1 m from the palm base, and the glyphosate herbicide was applied in a 2 m radius around palms. Mechanical weeding was conducted around each palm in a 2 m
radius from the palm base. Soil sampling was carried out at four core plots (OM1, OM2, OM3, and OM4) and four types of soil treatments (CH, CW, RH, and RW) in each core plot. Soil samples were taken from each soil treatment and were replicated five times for each soil treatment, resulting in a total of 80 soil samples (Figure 1).

Soil samples were taken from a depth of ~10 cm (topsoil) with a soil corer (~7 cm in diameter), and the sampling point was about 1 m from the oil palm tree. Three cores were taken per subplot, mixed, freed from roots and stones by hand, and supplemented with RNAprotect (Qiagen, Hilden, Germany). Subsequently, the soil samples were stored in cool boxes on ice packs and transported to the laboratory in Indonesia. The soil samples were frozen and stored at -20°C until shipment to the laboratory in Goettingen, Germany. The soil samples were transported in frozen using ice packs to Germany, and the soil samples were stored at -80°C until further use.

2.2. DNA Isolation and Actinobacterial Specific 16S rRNA Gene Amplification

To analyze the community and diversity of soil actinobacteria, DNA was isolated from all 80 soil samples by using the PowerSoil® DNA Isolation Kit (Qiagen, Hilden, Germany). DNA yields were measured using a Nanodrop Spectrophotometer ND-1000 (Thermo Fisher Scientific, Massachusetts, USA).

Semi-nested amplification reactions were performed. The first amplification was done to amplify the Actinobacterial specific 16S rRNA full-length gene using a specific primer pair (27F 5’-AGAGTTTGATCCTGGCTCAG-3’ and 16Sact1114R 5’-GAGTTGACCCCGGRTAG-3’) as described in Martina et al. (2008). The first amplification was performed to amplify only the actinobacterial specific 16S rRNA gene. This process allows us to investigate only the community of Actinobacteria specifically. The second amplification was carried out to amplify the V3 to V4 region of the previously amplified 16S rRNA gene.
using the specific primer to identify Actinobacteria (341F 5'-TCGTCCGAGCAGTATGCTATAAGAGACAGCTACGTGGTATCTACC-3’ and 805R 5'-GTCTCGTGGGTCTAGTATGCTATAAGAGACAGCTACGTGGTATCTACC-3’). The primers had been combined with specific adapters for the subsequent sequencing process (Klindworth et al. 2013).

One soil sample from each soil treatment (CH, CW, RH, RW) was chosen randomly as a control. Only one amplification reaction was performed on control samples. The amplification was performed to directly amplify the hypervariable V3 to V4 region of the 16S rRNA gene. The specificity of the primer used was investigated to increase the possibility of actinobacterial specific 16S rRNA gene amplification. The V3-V4 hypervariable regions can analyze the soil Actinobacteria (Schuwirth et al. 2005; Bukin et al. 2019).

The reaction mixture for the first amplification (25 µl total volume) contained 5 µl 5x GC buffer, 1 µl primer 27F, 1 µl primer 16Sact1114R, 0.2 µl MgCl₂, 2.5 µl DMSO, 1 µl dNTPs, 0.5 µl polymerase, 11.8 µl DEPC water, and 2 µl template DNA. The thermal cycling for amplification of actinobacterial specific 16S rRNA genes was set up for 30 cycles with an initial denaturation at 98°C for 1 minute, denaturation at 98°C for 45 seconds, annealing at 55°C for 45 seconds, elongation at 72°C for 30 seconds, and final elongation at 72°C for 5 minutes. Amplicons were purified using MagSi® NGSPREPplus (Magna Medics, Wiesenbach, Germany). Purified DNA was estimated by using a Nanodrop Spectrophotometer ND-1000 (Thermo Fisher Scientific, Massachusetts, USA).

The second amplification was performed similarly to the first amplification except the volume used for MgCl₂ was 0.75 µl, 1.25 µl DMSO, 0.5 µl dNTPs, 0.25 µl polymerase, 14.75 µl DEPC water, and 0.5 µl template DNA.

The amplicons were purified using MagSi® NGSPREPplus (Magna Medics, Wiesenbach, Germany) before proceeding to the next sequencing stage. The Goettingen Genomics Laboratory used the Nextera DNA library kits (Illumina Inc., San Diego, USA) for library preparation and determined the hypervariable V3 to V4 region sequences actinobacterial specific 16S rRNA gene amplicons by using Illumina Miseq (Illumina Inc., San Diego, USA).

2.3. Analysis of 16S rRNA Gene Sequences

The resulting hypervariable V3 to V4 region of actinobacterial specific 16S rRNA gene sequences were processed and analyzed using QIIME 1.9 (Caporaso et al. 2010). Quality filtering was performed using fastp (Chen et al. 2018). Paired-end sequences were joined with PEAR 0.9.11 (Zhang et al. 2014). The remaining primer sequences were clipped with cutadapt 1.16. Additionally, size filtering, dereplication, denoising, and removal of the chimera sequences were performed with VSEARCH 2.8.0 (Rognes et al. 2016). All reads were mapped against the SILVA database 132 with the BLAST tool. Taxonomic classification was performed with QIIME script parallel_assign_taxonomy_blast.py. Determination of operational taxonomic units (OTUs) was performed at a genetic divergence of 3% (similarity 97%) with pick_open_reference_otsu.py based on SILVA 132 NR SSU database as reference (Quast et al. 2013). OTU tables were created using make_otsu_table.py. Singletons, chloroplasts, unclassified OTUs, and extrinsic domain OTUs were removed from the table by employing filter_otsu_table.py. Biodiversity and the rarefaction curve were calculated using QIIME script alpha_rarefaction.py. Non-metric multidimensional scaling (NMDS) was performed in R (R Development Core Team 2017) based on a weighted UniFrac distance matrix (Lozupone et al. 2011).

Significant differences between samples and controls were determined calculated with t-test analysis and ANOVA using R (R Development Core Team 2017). The same analysis was performed to determine the treatments (fertilization and weeding) that significantly influenced the diversity and community of soil Actinobacteria. The results were interpreted with a significance level of p <0.05 (significance level 5%).

3. Results

3.1. Diversity and Community Composition of Soilborne Actinobacteria

Eighty soil samples were successfully analyzed based on the V3 to V4 hypervariable region of the actinobacterial specific 16S rRNA gene. Sequencing the 16S rRNA gene from all sampling plots resulted in 7,948,649 reads and 6,807,533 high-quality reads, comprised of 1847 OTUs with 97% sequence identity (3% dissimilarity).

In the "samples soil" (nested-PCR) dataset, most of the classified sequences (93.4%) belong to phylum Actinobacteria. Like Planctomycetes, Proteobacteria, and others, the other phyla were smaller than 2% (Figure 2). Conversely in the "control soil" (single-PCR) dataset, Acidobacteria (25.5%), Proteobacteria (18.5%),
and *Chloroflexi* (14.7%) were the most abundant phyla. In the "control soil," the relative abundance of *Actinobacteria* is no more than 9.5%. The relative abundance of phylum *Actinobacteria* in "samples soil" is significantly different from the controls (p<0.05), with *Actinobacteria* as the dominant phylum.

The number of actinobacterial OTUs in soil samples was weeded by glyphosate was higher than the soil samples was weeded mechanically. Moreover, the alpha diversity indices Shannon, Simpson, and Chao1 were also higher in soil samples weeded by glyphosate. However, the statistical test confirmed that the number of OTUs, the alpha diversity indices Shannon, Simpson, and Chao1 in the four soil treatments did not show significant (p <0.05) differences (Table 1).

The similarity of the soilborne *Actinobacteria* diversity in the four different soil treatments was confirmed with non-metric multidimensional scaling (NMDS, Figure 3). The NMDS plot also explained that the fertilization and weeding treatments did not affect the diversity of soilborne *Actinobacteria* in the oil palm plantations.

### 3.2. Effects of Fertilizer and Weeding Treatments on *Actinobacteria* Community

Around 50% of *Frankiales* consistently dominated in the four different soil conditions. The community composition of soilborne *Actinobacteria* in the four different soil treatments showed similar trends (Figure 4). The abundance of order *Micromonosporales*, IMCC26256, *Microtrichales*, *Micrococcales*, *Corynebacteriales*, OTU-97-2, *Streptomycetales*, *Propionibacteriales*, and *Kineosporiales* in the four

![Figure 2. Communities of soil bacteria in PTPN VI oil palm plantation Jambi Sumatra. Community compositions are displayed as relative abundance at the phylum level based on the sequences of the 16S rRNA gene (control: single-PCR, sample: nested-PCR)](image)

![Figure 3. Non-metric multidimensional scaling (NMDS) of soilborne *Actinobacteria* in four different soil treatments in the oil palm plantations Jambi, Sumatra based on weighted Unifrac distance matrices](image)

<table>
<thead>
<tr>
<th>Soil samples</th>
<th>Number of reads</th>
<th>Alpha diversity indices</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>High-quality</td>
</tr>
<tr>
<td>Conventional –Herbicide (CH)</td>
<td>1,858,239</td>
<td>1,622,538</td>
</tr>
<tr>
<td>Conventional-Mechanical (CW)</td>
<td>2,292,847</td>
<td>1,967,018</td>
</tr>
<tr>
<td>Reduce-Herbicide (RH)</td>
<td>1,941,323</td>
<td>1,755,690</td>
</tr>
<tr>
<td>Reduce-Mechanical (RW)</td>
<td>1,856,240</td>
<td>1,462,287</td>
</tr>
</tbody>
</table>
different soil treatments also resulted in similar patterns.

Statistical tests ANOVA confirmed the interaction between fertilization and weeding treatments had no significant effect (p<0.05) on the community composition of soilborne Actinobacteria in the oil palm plantation. Furthermore, the abundance of Kineosporiales was significantly (p<0.05) affected by NPK fertilizer. The higher concentration of NPK fertilizer used, the greater abundance of Kineosporiales (1.25% in reduced fertilization increased to 2.2% in conventional fertilization).

4. Discussion

4.1. Diversity and Community Composition of Soilborne Actinobacteria

The presence of specific bacterial phyla in the plantation’s soil was reported to have many important ecological functions. Proteobacteria and Acidobacteria were dominant phyla in the oil palm plantation Jambi, Sumatra. Phylum Proteobacteria and Acidobacteria were previously reported as generally high abundant in soils, and they have an important role in the decomposition of soil carbon (Hansel et al. 2008; Leff et al. 2012; Schneider et al. 2015; Wijayanti et al. 2019). Furthermore, Chloroflexi was also found in the oil palm plantation soil. The Chloroflexi was mainly associated with oil palm and crop management in the agricultural system (Bouskill et al. 2013; Orr et al. 2015; Wijayanti et al. 2019). The abundance of Actinobacteria in the oil palm plantations soil was less than Proteobacteria, Acidobacteria, and Chloroflexi. According to Yun et al. (2016), Actinobacteria was more abundant in soils with a neutral or alkaline pH. However, previous studies confirmed that the oil palm plantations soil in Jambi, Sumatra has a low pH of about 4.5 (acidic soil) (Wijayanti et al. 2019).

The actinobacterial specific 16S rRNA gene primer has been successfully amplified only the actinobacterial 16S rRNA gene. The results were indicated by the significant differences in the abundance phylum Actinobacteria between "soil samples" (nested-PCR) and control soil" (single-PCR). In the "samples soil" dataset, most of the classified sequences belong to phylum Actinobacteria. According to the previous studies, Martina et al. (2008) reported that the primers 16Sact1114R and
27F are specific primers to amplify actinobacterial specific 16S rRNA genes. The primers were able to identify Actinobacteria to the genus level.

The other actinobacterial-specific primers are Com2xf/Ac1186r (Schafer et al. 2010) and S-C-Act-0235-a-S-20/S-CAct-0878-a-A-19 (Stach et al. 2003). The Actinobacteria specific primer detected around 87% sequences were assigned to actinobacterial genera. Tang et al. (2016) confirmed that 75 of 425 clones belonged to Actinobacteria by employing the primers. Compared with the two actinobacterial-specific primers, the primer used in this study (27F/16Sact1114R) was expected to have a higher level of specificity because by using the primers, the number of Actinobacteria detected was higher. However, further research is still needed to compare the level of specificity of all the actinobacterial-specific primers systems. Indeed, the use of actinobacterial-specific primers increased the amplification of actinobacterial 16S rRNA genes, although some 16S rRNA genes from other bacterial phyla were still amplified in smaller amounts.

The diversity and species richness of soilborne Actinobacteria in the four different soil treatments in the oil palm plantation was similar. It revealed that the utilization of NPK fertilizers and glyphosate herbicide in the oil palm management system did not affect the diversity of soil Actinobacteria. This result corresponds to the studies that reported that the diversity of Actinobacteria was not affected by crop management. However, the diversity and abundance of soil Actinobacteria in the long-term fertilization field were primarily affected by the sampling time and seasonal variation (Chhabra et al. 2013; Orr et al. 2015). In this study, we collected the samples in the same year. Therefore the diversity of soil Actinobacteria did not differ significantly.

We expected the Actinobacteria was indigenous microbes in the oil palm plantations soil. The Actinobacteria already existed in the soil before the NPK fertilizer and herbicide were applied to the oil palm plantations system. Furthermore, the previous study reported that ancient actinobacterial DNA showed no damage (Zaremba-Niedzwiedzka and Andersson 2013). Actinobacteria are microbes that can survive and adapt well in various environments. However, the ecological function of actinobacteria is mostly unknown. Therefore, the diversity of soil Actinobacteria based on 16S rRNA gene sequences in the four different soil treatments was similar. Tang et al. (2016) suggested that each ecologically similar study site shows similar Actinobacteria diversity due to identical environmental conditions. We collected soil samples from one study site in this study, although there were four different treatments. It might be that the causes of soil Actinobacteria's diversity did not differ significantly.

4.2. Effects of Fertilizer and Weeding Treatments on Actinobacteria Community

The community composition of soilborne Actinobacteria in the four different soil treatments consistently was dominated by Frankiales. The order Frankiales was soil Actinobacteria found abundantly in Sumatra’s forest and oil palm plantations. Berkelmann et al. (2018) reported that Frankiales dominated the soil bacterial community in rubber forest and oil palm plantations in Jambi, Sumatra. Moreover, Frankiales was also reported to be the most abundant Actinobacteria in the rainforest soil in Sumatra (Schenider et al. 2015). In general, Frankiales are related to Actinobacteria that are symbiotic with plant roots and play a role in forming the nodules for nitrogen fixation and related to the nitrogen cycle in the environment (Franco-Correa et al. 2010). The Frankiales’ existence in the soil of palm plantations was also related to the application of NPK fertilizers.

The community of soilborne Actinobacteria in the oil palm plantations was also composed of Micromonomosporales, IMCC26256, Microtrichales, Micrococcales, Corynebacteriales, OTU-97-2, Streptomycetales, Propionibacteriales, and Kineosporiales. The existence of order Micrococcales and Streptomycetales was related to the fertilization system. Micrococcal and Streptomycetales were identified as a bioindicator for fertilizer treatments in agricultural soil (Harkes et al. 2019), although this study revealed that the fertilizer treatments did not influence the abundance of Micrococcales and Streptomycetales. Additionally, Propionibacteriales were reported predominately also found in agricultural soil. Unfortunately, the important role of these taxa is still not known. Micromonomosporales could dissolve phosphate in the environment (phosphate solubilizers) (Wang et al. 2016; Yeager et al. 2017). Therefore, the abundance of Micromonomosporales in the plantation soil is supposedly related to NPK fertilizer application.

The interaction between fertilization and weeding treatments did not significantly affect the community composition of soilborne Actinobacteria in the oil palm plantation. Furthermore, the abundance of
The microbial community is not fully known. The range of sensitivity to glyphosate within the soil varies depending on the history exposure, the concentration of herbicide used, and the particular taxa of soil microbes themselves. Additionally, Duke and Powles (2008) confirmed no significant differences in diversity and community composition of soilborne Actinobacteria among the four different treatments in oil palm plantations. Active bacterial studies (based on RNA) are preferable to investigate the diversity and community composition of soilborne Actinobacteria.

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