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ORIGINAL PAPER

Analysis of rhizobacterial community associated with the occurrence of *Ganoderma* basal stem rot disease in oil palm by Illumina next-generation sequencing

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Abstract

The fungus *Ganoderma boninense* is a causal pathogen of basal stem rot, a serious disease of oil palm plantation systems. As previously observed, some oil palm trees show no appearance of disease symptoms (asymptomatic oil palm), although they have grown close to a tree that showed severe symptoms of basal stem rot disease (symptomatic oil palm). The microbial community difference between asymptomatic and symptomatic oil palm will help understand disease suppression. Thus, in this study, rhizosphere soil was sampled around asymptomatic (OP − G) and symptomatic (OP + G) oil palm trees in *Ganoderma*-infected oil palm orchards. Illumina next-generation sequencing (NGS), bioinformatics analysis, bacterial diversity, and soil physicochemical properties were evaluated. The results demonstrated that soil physicochemical properties and species richness around rhizosphere soil of OP − G and OP + G samples were not significantly different. The age of the oil palm trees and oil palm variety showed negligible correlation and were not significant with bacterial diversity. However, the top ten most abundant analysis of the bacterial communities showed that phyla *Actinobacteria* and *Firmicutes* were significantly increased in rhizosphere soil around OP − G samples relative to the OP + G samples. The unique operational taxonomic units (OTUs) of OP − G (2137) were higher than in the OP + G samples (1747 OTUs). These bacterial communities have been reported as biological control agents and/or plant growth-promoting rhizosphere bacteria that are related to disease suppression. Thus, the data provided are useful for developing suppressive soil to biologically control *G. boninense*.

Keywords Oil palm · Rhizobacterial community · Illumina next-generation sequencing · *Ganoderma* basal stem rot · Disease suppression

Introduction

Oil palm (*Elaeis guineensis*) is a plant with economic importance. Palm oil extracted from its fruit is used in cooking, biofuel production, pharmaceuticals, and cosmetics, among other uses. One of the main soil organisms in oil palm plantation ecosystems that acts as a soilborne pathogen to oil palm is *Ganoderma boninense,* which causes basal stem rot disease (Nusaibah et al. 2016). Basal stem rot disease in oil palm is a serious problem in Indonesia and Malaysia, globally first and second ranked countries in crude palm oil production, respectively (Colchester and Chao 2011). Similar problems are experienced in Thailand and in many other countries in Southeast Asia. A productivity decline in oil palm plantations has been a concern. Losses of revenue in the palm oil industry and significant economic losses have been reported (Nusaibah et al. 2016; Olaniyi and Szulczyk 2020), attributed to *G. boninense* that kills the oil palm trees. In some Southeast Asian countries, economic losses caused by this pathogen are estimated at around 500 million USD per year (Hushiarian et al. 2013).

From our observations in 2019, oil palm trees both with and without basal stem rot disease symptoms are found in the same orchard. The question is why did the pathogen not establish or established itself in but caused

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no damage to some oil palm trees, although the pathogen may persist in the soil, and other nearby trees show severe symptoms of basal stem rot disease. Corato (2020) suggested that plant diseases caused by soilborne pathogens can be effectively suppressed by abiotic and biotic factors. Anothai and Chairin (2020) found that soil physicochemical properties in oil palm plantation systems, such as organic matter, organic carbon, and soil pH, have a positive relationship with defensive enzymes in oil palm, inhibiting *Ganoderma* fungal infection and could suppress basal stem rot disease. As regards biotic factors, rhizosphere bacteria in the soil relate to plant disease occurrence and have been reported to play a key role in suppressing soilborne pathogens (Gómez et al. 2017). Bacterial antagonists such as *Bacillus* spp., *Pseudomonas* spp., *Streptomyces* spp. and *Burkholderia* spp. have been utilized against *G. boninense* (Susanto et al. 2005; Irma et al. 2018; Lim et al. 2018; Sujarit et al. 2020). Several microorganisms can efficiently control the plant pathogens in vitro or in greenhouse conditions, but the majority have failed in reported field environment tests (Alabouvette et al. 2009). Also, disease suppression is generally attributed to microbial communities rather than to only one microbial species (Gómez et al. 2017).

Recent next-generation sequencing (NGS) methods, such as Illumina-based techniques, may provide a more direct way of detecting microbial taxa in soil, especially the changes in low-abundance species, and to explore the total microbial community in the environment (Salipante et al. 2014). Nimnoi and Pongsilp (2020) used this method on marine bacterial communities related to the type of land use. Jiang et al. (2019) used the NGS for studying the soil microbial community and suggested that different microbial community compositions in soil attached to healthy and rotted roots were caused by fungal pathogens of American ginseng. In addition, Utomo et al. (2018) also used this method to find out a draft genome sequence of *G. boninense* strain G3 isolated from oil palm trees.

Many studies have demonstrated useful assessments of soil microbial community and tree crop health by NGS. However, very few papers have used NGS to assess the possibility that soil bacterial communities could suppress basal stem rot disease and possibly control *Ganoderma* in an oil palm plantation (Goh et al. 2020). Thus, to clarify the relationship of soil bacterial community with the basal stem rot disease occurrence in oil palm trees, the present study collected rhizosphere soil around symptomatic and asymptomatic oil palm trees in *Ganoderma*-infected oil palm orchards. Illumina NGS results were subjected to bioinformatics analysis, and bacterial diversity was evaluated along with soil physicochemical properties.

Materials and methods

Study area and sampling design

Oil palm orchards in the major oil palm plantation areas in southern Thailand, i.e., Chumphon (location C), Krabi (location K), and Surat Thani provinces (location S), were studied from September 2018 to March 2019. General information on the studied orchards is shown in supplementary Table S1. Six oil palm trees from each orchard were selected, three of which were in the symptomatic oil palm (OP + G) group, referring to oil palms presenting symptoms of basal stem rot disease and fruiting bodies (basidiocarp) of *Ganoderma,* while the other three were without fruiting bodies and looked healthy constituting the asymptomatic oil palm (OP − G) group. The OP − G trees were randomly selected within 20 m radius from the OP + G trees. Ten sampling points per tree at 15 cm radial distance from the basal stem of the tree were selected for collecting rhizosphere soil and were taken from the upper soil horizon (0–15 cm) at each tree using a soil probe (Anothai and Chairin, 2020), then the soil samples were pooled before determining soil physicochemical properties and bacterial communities.

Soil physicochemical properties

Soil physicochemical properties determined included electrical conductivity (EC), soil moisture, pH, organic matter (OM), organic carbon (OC), and macronutrient nitrogen (N), phosphorus (P), and potassium (K). These were analyzed at the Central Analysis Center, Faculty of Natural Resources, Prince of Songkla University, Hat Yai, Songkhla, Thailand. OM and OC were analyzed by Walkley and Black (1934) method, nitrogen was analyzed by Kjeldahl method (Kjeldahl 1883), phosphorus was analyzed by a spectrophotometric method (Avila-Segura et al. 2007), and extraction with ammonium acetate was developed for exchangeable K evaluation (Normandin et al. 2008).

Soil DNA extraction and Illumina next-generation sequencing

For each soil sample, total genomic DNA was extracted using the TIANamp Soil DNA Kit (TianGen, China), following the manufacturer's instructions. PCR amplifications were conducted with the 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) primer set that amplifies the V4 variable region of 16S rRNA gene (Apprill et al. 2015). The quality and quantity of the PCR product was verified by agarose gel electrophoresis. The PCR products were purified using a

Qiagen gel extraction Kit (Qiagen Inc., USA). The libraries were generated with TruSeq DNA PCR-Free sample preparation Kit (Illumina Inc., USA). Amplicon was sequenced on Illumina HiSeq paired-end platform (HiSeq 2500 PE250 sequencing system, Illuminar Inc., USA) following the manufacturer's instructions. The fastq data were returned and deposited in the Sequence Read Archive (SRA) of National Center for Biotechnology Information under BioProject accession number PRJNA636220.

Data processing and bioinformatics analysis

Paired-end reads were merged by using the FLASH program Version 1.2.7 (Magoč and Salzberg 2011) and quality filtering on the raw tags was performed under specific filtering conditions to obtain high-quality clean tags according to the Qiime (V 1.7.0) (Caporaso et al. 2010). The tags were compared with the reference database (Gold database) using UCHIME algorithm to detect chimera sequences (Edgar et al. 2011) and then the chimera sequences were removed: effective tags were finally obtained. Regarding the operational taxonomic units (OTUs) clustering and species annotation, Uparse software v7.0.1001 (Edgar 2013) was used for sequence analysis of all the effective tags. The sequences with ≥ 97% similarity were assigned to the same OTUs and a representative sequence for each OTU was screened for further annotation. For each representative sequence, Mothur software was applied against the SSUrRNA database of SILVA Database (Wang et al. 2007) for species annotation at each taxonomic level at threshold level 0.8 ~ 1 (Quast et al. 2013). MUSCLE program Version 3.8.31 was used to get the phylogenetic relationship of OTUs sequences (Edgar 2004).

Statistical analysis

For bacterial diversity, Chao1 and ACE (Abundance-based coverage estimator) estimators were used for analyzing community richness, and Shannon and Simpson indices were used for analyzing community diversity, while Good's coverage was used for calculating the index of sequencing depth. Rarefaction data were calculated by the QIIME software and displayed by the R software (V 2.15.3) (Core Team R 2013). The unweighted pair group method with arithmetic mean (UPGMA) was used in hierarchical clustering to interpret the distance matrix using average linkage, in QIIME software. The analysis of similarities (ANOSIM) was used for non-parametric data to determine whether the bacterial community structures significantly differ between groups or within groups. Analysis of molecular variance (AMOVA) was performed using Mothur software (V 1.36.1). Pearson correlation analysis was used to test the relationship between the diversity parameters and plant physical properties. Soil parameters, alpha diversity indices, and physicochemical properties of OP + G and OP − G for each location were subjected to an analysis of variance (ANOVA) combined with Tukey's multiple range test, performed with the SPSS software (V.16.0). Statistical significances required an alpha level of 0.05.

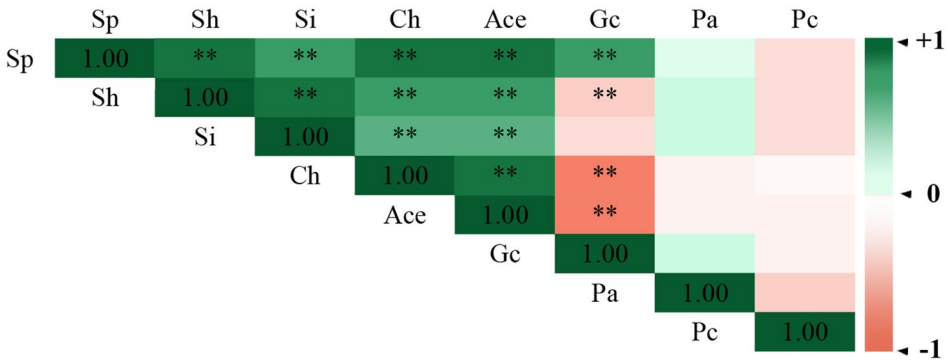
Results

Field observation of *Ganoderma*-infected oil palm

The symptomatic trees (OP + G) were oil palms presenting symptoms of basal stem rot disease, i.e., unopened spears at the top of a tree canopy, yellowing and early necrosis on leaves, reclining of lower leaves to form a skirt-like crown, and fruiting bodies (basidiocarp) of *Ganoderma* presenting at the base of that oil palm tree. The upper surface of the basidiocarp cap takes up a bracket shape with reddish to orange color on its outer surface, white colored on its terminal region and with confluent formation of visible hymenium (pore) on its underside. The pore surface was whitish and round-shaped pores with diameter around 0.1 mm were observed at the underside of the mature basidiocarp. Asymptomatic oil palm trees (OP − G) were without fruiting bodies and looked healthy.

Sequence analyses and diversity indices

A total of 3,015,756 raw reads were obtained from 30 DNA samples (10 sampling points/replicate and 3 replicates/sample). After tag merge and quality control, a total of 2,828,835 clean tags (93.85% of raw reads) were obtained. The potential chimera tags were removed with the UCHIME algorithm, resulting in a total of 1,962,339 taxon tags. The tags with ≥ 97% similarity were grouped into the same OTU. A total of 13,349 OTUs were obtained from all samples, with a mean Good's coverage of 97.24 ± 0.00%. ACE and Chao1 that indicate species richness, as well as Shannon–Weaver and Simpson that indicate diversity were analyzed. The soil physicochemical properties in rhizosphere soil from each location are also shown in supplementary Table S2. No significant difference was found between Chao1, Shannon–Weaver and Simpson indexes or soil physicochemical properties in the *Ganoderma*-infected oil palm orchards sampled. However, ACE index of location S2 was significantly lower than that of location C. Age of oil palm trees and oil palm variety showed negligible correlation (correlation coefficient 0.00–0.30 or − 0.30) with community richness and diversity index when analyzed by Pearson correlation and no significant difference was found in these parameters (Fig. 1). Moreover, when compared between OP + G and OP − G samples, the soil physicochemical



**. Correlation is significant at the 0.01 level (2-tailed).

Fig. 1 Pearson correlations between bacterial diversity indices around rhizosphere soil in *Ganoderma*-infected oil palm orchards and plant properties ($n = 30$). *Sp* observed species, *Sh* Shannon–Weaver index, *Ch* Chao1 index, *ACE* Abundance-based coverage estimator, *Gc* Good's coverage, *Pa* Age of oil palm tree, *Pc* Oil palm variety

properties and the bacterial diversity were not significantly different with an alpha level 0.05 (Table 1).

Illumina NGS and bacterial community structure

Supplementary Fig. S1 presents the rarefaction curves of samples that were steep, indicating that the samples were randomly collected. As shown in the Venn diagram of Fig. 2, the OP − G samples had 2731 OTUs common to all study sites. The location C had the most unique OTUs (1033 OTUs), followed by location S1 (679 OTUs), location K (653 OTUs), location S3 (464 OTUs) and location S2 (410 OTUs) in rank order, while the Venn diagram of OP + G samples differed from that of OP − G samples. Moreover, when comparing OP − G and OP + G samples, the average unique OTUs of OP − G was 2137 higher than for OP + G samples (1747 OTUs).

The top ten most abundant phyla among the five study locations had different patterns, as depicted in Fig. 3. The dominant bacterial phyla were *Proteobacteria* in all samples, ranging between 28.74 and 40.92%, followed by *Acidiobacteria* (10.88–38.27%), *Actinobacteria* (3.92–25.29%), *Bacteroidetes* (2.38–13.81%), *Verrucomicrobia* (2.12–9.71%), *Thaumarchaeota* (0.36–4.19%), *Firmicutes* (1.33–5.02%), *Gemmatimonadetes* (1.39–3.54%), *Chloroflexi* (2.01–3.53%), *Nitrospirae* (0.27–1.61%) and others (3.68–7.44%). When comparing abundant phyla between OP − G and OP + G samples, it was found that the *Actinobacteria* and *Firmicutes* of OP − G samples were higher than in OP + G samples, with significant difference at alpha 0.05 (Fig. 4). The distribution of bacterial genera in OP − G and OP + G samples in all locations is shown in Fig. 5. The colors in the heat map indicate relative abundances from low (deep blue color) to high (red color) in the bacterial community. Soil samples of OP − G from location S2 showed more intensity in many genera than the other samples. The most abundant genera in OP − G samples were *Burkholderia*, *Cellulomonas*, *Dyella*, *Lactobacillus, Nocardioides, Paenibacillus, Rubrobacter* and *Streptomyces*.

Discussion

From the previous reports regarding an oil palm plantation ecosystem, almost all organisms studied so far have lower species richness, including wood-inhabiting fungi, plants, litter invertebrates, dung beetles, ants, amphibians, lizards, birds, and mammals. Not only is the species richness lower, but also the species that are present are more likely to be common, generalist species (Dislich et al. 2017). Furthermore, Lo and Chong (2020) analyzed the soil microbial diversity in an oil palm plantation in Malaysia in relation to basal stem rot disease by using Illumina MiSeq metagenomic technique and reported that the most abundant phyla were *Proteobacteria, Acidobacteria, Actinobacteria*, and *Verrucomicrobia*. However, that recent report does not address the possibility of rhizosphere bacteria suppressing basal stem rot disease.

In the present study, the variation of age and varieties of oil palm had a weak correlation with the bacterial community in the studied area. Bacterial community composition differs between the rhizosphere soil of asymptomatic oil palm trees and those with severe symptoms of basal stem rot disease, while the soil physicochemical properties, bacterial diversity and species richness index from rhizosphere soils did not significantly differ between oil palms with or without basal stem rot disease, but there were more unique OTUs for OP − G than for OP + G samples. From the interview data, the farmers in studied sites did not adopt any of the practices to control basal stem rot disease, which could have caused some changes in soil properties and bacterial communities in rhizosphere soil of OP − G than for OP + G samples. Berkelmann et al. (2020) reported that soil bacterial community structures were related to altered management practices, which affected nutrient cycling and soil physical properties in an oil palm plantation.

The number of species from soil sample from location S2 was low in ACE index; however, the relative abundances were high in many bacterial genera as shown in the species abundance heatmap. Most of the genera in location S2 were

Table 1 Soil physicochemical properties, community richness and diversity indices analyzed for symptomatic (OP + G) or asymptomatic (OP – G) groups of oil palm trees

Group	Soil physicochemical properties								Observed species	Community richness		Community diversity	
	OM (%)	OC (%)	N (%)	P (mg kg^{-1})	K (mg kg^{-1})	pH	EC (ppm)	Moisture (%)		Chao1	ACE	Shannon	Simpson
OP + G	6.22 ± 2.38[a]	3.62 ± 1.39[a]	0.26 ± 0.11[a]	130.54 ± 123.34[a]	409.71 ± 334.35[a]	5.17 ± 0.65[a]	47.74 ± 35.62[a]	27.10 ± 5.21[a]	3482.19 ± 643.97[a]	4417.92 ± 849.08[a]	4486.87 ± 852.91[a]	9.73 ± 0.69[a]	0.995 ± 0.01[a]
OP – G	4.53 ± 1.34[a]	2.63 ± 0.78[a]	0.19 ± 0.06[a]	166.73 ± 206.17[a]	203.73 ± 119.17[a]	5.14 ± 0.66[a]	30.38 ± 27.57[a]	28.87 ± 6.53[a]	3570.69 ± 604.92[a]	4503.49 ± 718.42[a]	4579.39 ± 706.37[a]	9.81 ± 0.63[a]	0.996 ± 0.00[a]

Data shown as mean ± standard deviation and values with the same letter within a column are not significantly different ($p > 0.05$) according to independent sample *t* test

Cellulomonas, *Lactobacillus, Paenibacillus* and *Rubrobacter*, while the other genera were limited in number and had poor distribution throughout the soil. The top ten most abundant phyla in bacterial community analysis showed that *Actinobacteria* and *Firmicutes* were significantly increased in rhizosphere soil around asymptomatic oil palms relative to the symptomatic oil palm samples. In addition, *Proteobacteria* was the dominant bacterial phylum in both types of samples, ranging within 28.74–40.92%. These differences in bacterial communities may relate to the suppression of basal stem rot disease. In observations of similar kind by Jiang et al. (2019) or, more recently, by Yin et al. (2021), the composition of bacterial community may affect disease-suppression ability and reduce plant disease occurrences. Rhizosphere bacteria in soil have been reported as having a key role in suppressing soilborne pathogens (Gómez et al. 2017). Yang et al. (2017) suggested that the plant health related to the soil microbial diversity and some potential plant-beneficial microbial groups, e.g., *Bacillus* and *Actinobacteria*, could act as network key taxa for reducing the invasion by soilborne pathogens.

Bacterial genera of *Actinobacteria* phylum were detected as most abundant in the rhizosphere soil around asymptomatic oil palm trees, especially the genera *Streptomyces, Cellulomonas, Kocuria, Blastococcus, Rubrobacter* and *Nocardiodes,* in this study. *Actinobacteria* are a phylum of Gram-positive bacteria that produce a large and diverse array of bioactive compounds inhibiting the development of pathogens in soil (Sharma et al. 2005). *Streptomyces* and *Cellulomonas* can inhibit the development of the fungal pathogen *Helminthosporium solani* on potato tubers (Martinez et al. 2006). *Nocardioides* reduce foliar disease of tomato by inhibiting spore germination of phytopathogenic fungi (Filho et al. 2008). *Streptomyces* isolated from soil have significant antifungal ability against *Ganoderma* by producing antimicrobial compounds, abguinomycin A, leptomycin A (Sujarit et al. 2020), ribostamycin, benzylmalic acid, landomycin B and salinomycin (Lim et al. 2018). However, while *Blastococcus*, *Rubrobacter* and *Kucuria* are rhizobacteria in many plantation systems, only little information of their antimicrobial activities is available in the context of orchard soil (Sun et al. 2014).

Paenibacillus and *Lactobacillus* were detected as the dominant genera of phylum *Firmicutes* in rhizosphere soil around OP-G samples, in this study. There are several reports about the *Firmicutes* and their ability to control fungal pathogens (Ek-Romos et al. 2019). Zhou et al. (2008) found that *Paenibacillus* strongly inhibited *Penicillium expansum* by producing antifungal protein 4517 Da. *Lactobacillus* produced cyclic dipeptides, *cis*-cyclo (L-Val-L-Pro) and *cis*-cyclo (L-Phe-L-Pro) that showed significant anti-*Ganoderma* activity (Kwak et al. 2014). Moreover, phylum *Firmicutes* is reported as a source of

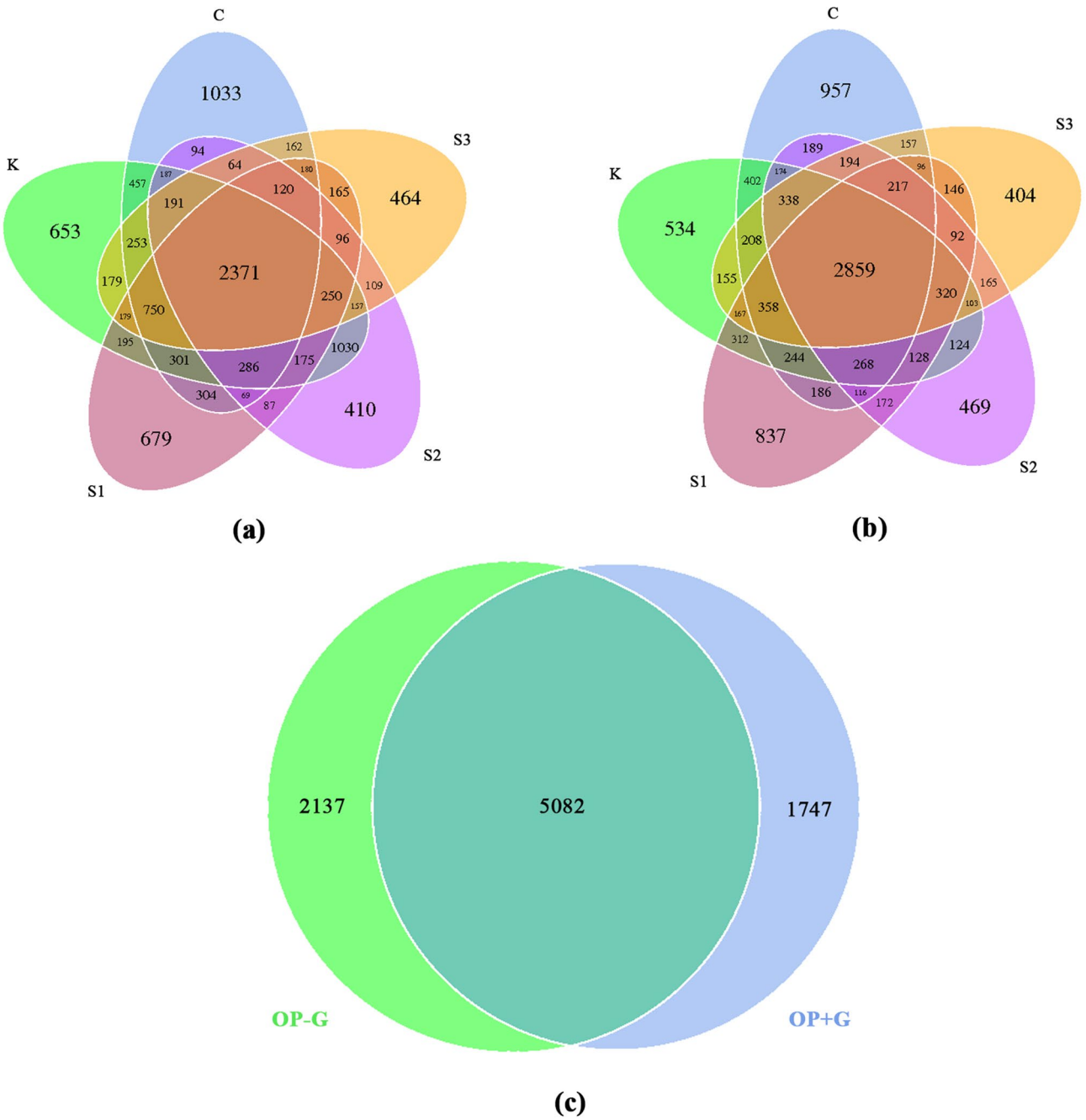


Fig. 2 OTUs Venn diagram analysis of bacterial communities in rhizosphere soil from locations C, K, S1, S2 and S3; asymptomatic oil palm trees (**a**), basal stem rot disease oil palm trees (**b**), and comparison of OTUs between OP − G and OP + G samples (**c**)

plant growth-promoting rhizobacteria (PGPR) and phylum *Proteobacteria* as well. These PGPR have mechanisms to promote plant growth and can potentially be used for the biological control of plant diseases (Campant et al. 2005). In this study, the dominant bacterial genera members of *Proteobacteria,* i.e., *Dyella*, *Burkholderia* and *Escherichia,* were detected as highly prevalent in rhizosphere soil of asymptomatic oil palm trees. There have been many suggestions of potential use of PGPR for stimulating plant growth and managing plant health. As reported by Campant et al. (2005), Benedezu et al. (2012), Giorgio et al. (2015) or, more recently, by dos Santos et al. (2020), the mechanisms of PGPR for suppressing plant diseases include competitive root colonization, production of iron-chelating siderophores, antibiotics, biocidal volatiles, lytic enzymes for degrading fungal cell walls, detoxification

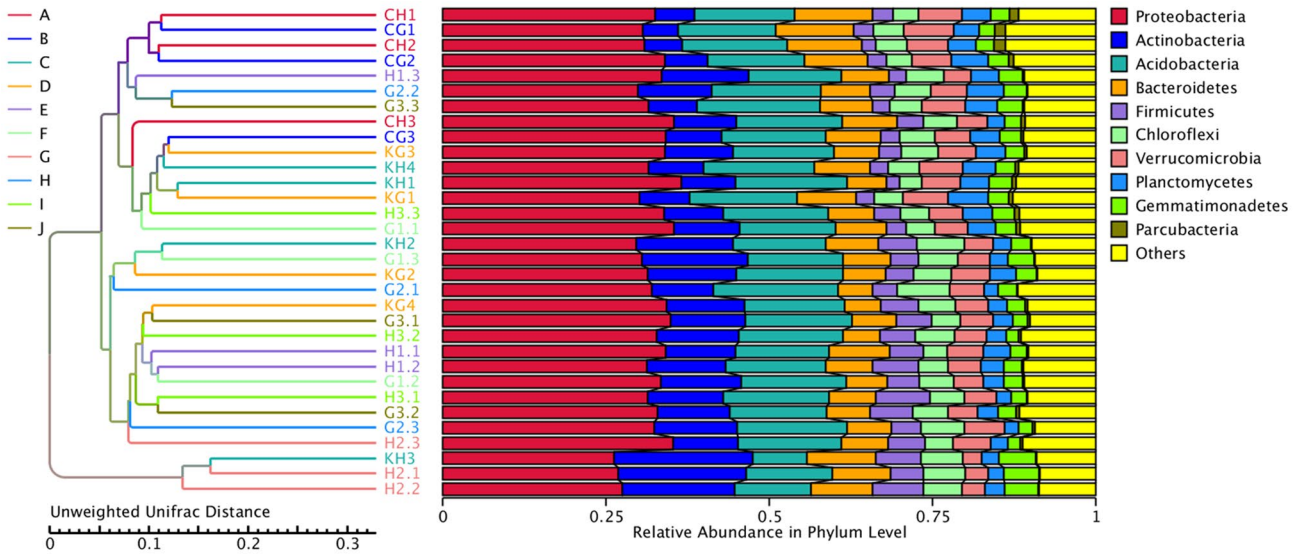


Fig. 3 The UPGMA dendrogram of relative abundances at phylum level from three samples for each location when divided into symptomatic oil palm (OP + G) and asymptomatic oil palm (OP-G) groups. **A** Location C (OP − G), **B** location C (OP + G), **C** location K (OP − G), **D** location K (OP + G), **E** location S1 (OP − G), **F** location S1 (OP + G), **G** location S2 (OP − G), **H** location S2 (OP + G), **I** location S3 (OP − G) and **J** location S3 (OP + G)

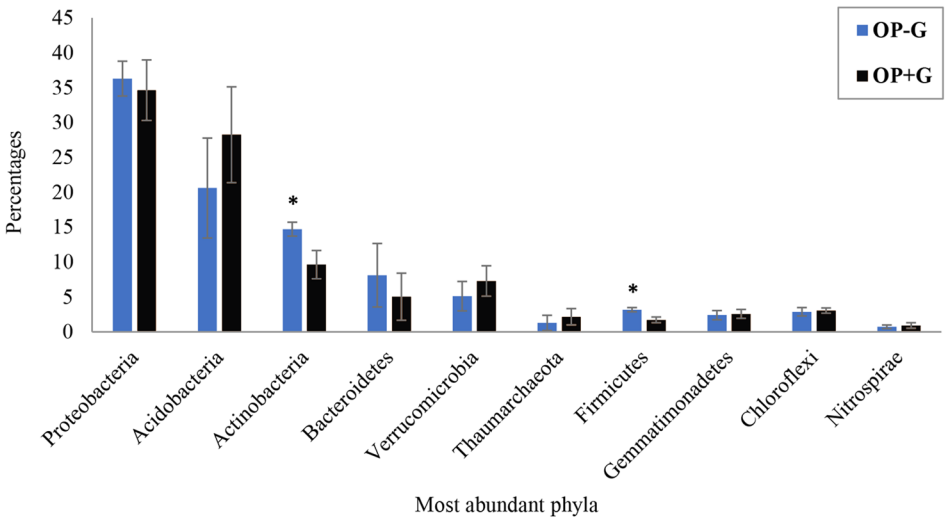


Fig. 4 Percentages of the most abundant phyla from rhizosphere soil of symptomatic oil palm (OP + G) and asymptomatic oil palm (OP − G) samples. Data shown as mean ± standard deviation (error bar) and * indicates significant difference ($p < 0.05$) according to independent samples *t* test

of pathogen virulence factors, and induction of systemic resistance in the host plant against pathogen infection.

In conclusion, our study found that *Ganoderma*-infected oil palm orchards in the studied sites in Chumphon, Krabi and Surat Thani provinces, in southern peninsular Thailand, have a large bacterial community that may be associated with basal stem rot disease occurrence. The unique OTUs and bacterial phyla, *Actinomyces* and *Firmiculate*, in rhizosphere soil sampled around asymptomatic oil palm were higher than for oil palm that showed severe symptoms of basal stem rot disease. These bacterial communities have been reported as the biological control and/or plant growth-promoting rhizosphere bacteria. The data provided are useful for developing suppressive soil to biologically control *G. boninense*. Furthermore, in the future the factors, e.g., cultural practicesand others living in soil, in relation with bacterial community need to be

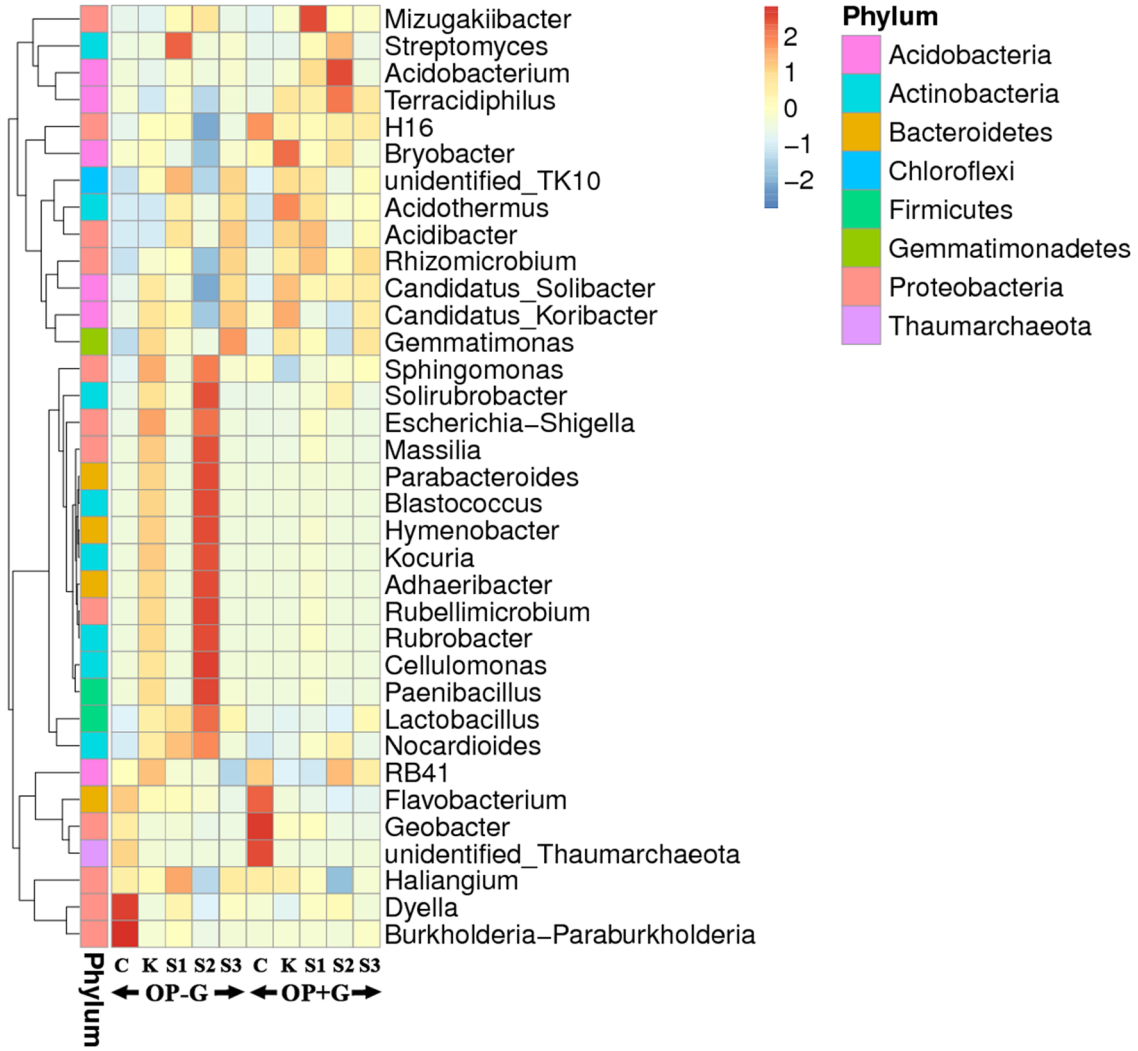


Fig. 5 Species abundance heatmap analysis of genus distribution in symptomatic oil palm (OP + G) and asymptomatic oil palm (OP − G) samples in each location

tested for integrating into disease control with the suppressive soil.

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Author contributions JA and TC conceptualized and designed the study. TC experimented, collected the needed data, and wrote the draft of the manuscript. All the authors reviewed the manuscript and approved it for submission.

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Declarations

Conflict of interest All authors declare no conflict of interest.

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

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