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Research article

Revealing the role of Plant Growth Promoting Rhizobacteria in suppressive soils against *Fusarium oxysporum* f.sp. *cubense* based on metagenomic analysis

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ABSTRACT

Fusarium oxysporum f.sp. *cubense* (Foc) is a soil-borne pathogen causing fusarium wilt banana disease. Management of soil-borne disease generally required the application of toxic pesticides or fungicides strongly affect the soil microbiomes ecosystem. Suppressive soil is a promising method for controlling soil-borne pathogens in which soil microbiomes may affect the suppressiveness. The comparative analysis of microbial diversity was conducted from suppressive and conducive soils by analyzing whole shotgun metagenomic DNA data. Two suppressive soil samples and two conducive soil samples were collected from a banana plantation in Sukabumi, West Java, Indonesia. Each soil sample was prepared by mixing the soil samples collected from three points sampling sites with 20 cm depth. Analysis of microbial abundance, diversity, co-occurrence network using Metagenome Analyzer 6 (MEGAN6) and functional analysis using Kyoto Encyclopedia of Genes and Genomes (KEGG) was performed. Data showed the abundance of *Actinobacteria, Betaproteobacteria, Rhizobiales, Burkholderiales, Bradyrhizobiaceae, Methylobacteriaceae, Rhodopseudomonas palustris*, and *Methylobacterium nodulans* were higher in the suppressive than conducive soils. Interestingly, those bacteria groups are known functionally as members of Plant Growth Promoting Rhizobacteria (PGPR). The co-occurrence analysis showed *Pseudomonas, Burkholderia*, and *Streptomyces* were present in the suppressive soils, while *Bacillus* and more *Streptomyces* were found in the conducive soils. Furthermore, the relative abundance of *Pseudomonas*, *Burkholderia*, *Bacillus*, and *Streptomyces* was performed. The analysis showed that the relative abundance of *Pseudomonas* and *Burkholderia* was higher in the suppressive than conducive soils. Therefore, it assumed *Pseudomonas* and *Burkholderia* play a role in suppressing Foc based on co-occurrence and abundance analysis. Functional analysis of *Pseudomonas* and *Burkholderia* showed that the zinc/manganese transport system was higher in the suppressive than conducive soils. In contrast, the phosphate transport system was not found in conducive soils. Both functions are may be responsible for the synthesis of a siderophore and phosphate solubilization. In conclusion, this study provides information that PGPR may be contributing to Foc growth suppressing by releasing secondary metabolites.

1. Introduction

Banana (*Musa acuminata*) and plantain are rich in nutrients, including vitamins A and C, potassium, calcium, sodium, magnesium, and become one of the essential sources of energy (Ashokkumar et al., 2018). In 2017, global banana production reached 22.7 million tonnes with a value of USD 11 billion (Voora et al., 2020). It became the most critical commodity export that provides a livelihood for millions of farmers and households (Calberto et al., 2015).

Nowadays, bananas and plantain were seriously threatened by the soil-borne fungus *Fusarium oxysporum* f.sp *cubense* (Foc) (Mostert et al., 2017). It caused significant production losses in Taiwan, Malaysia, Northern Australia (Su et al., 1986), and more than 80% of the world's banana production is highly dependent on the susceptibility of plants to Foc (Rodriguez et al., 2014). In 2011, Hermanto et al. (2011) reported that the incidence level of Foc causes losses of 1.21 trillion rupiah per year due to over 65% of 40 banana varieties from 15 provinces were infected by Foc (Maryani et al., 2019).

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Several handling methods to control Foc have been used, such as fumigation and fungicides, but they were considered less effective since they cannot remove Foc chlamydospores (Harrach et al., 2013). Foc resistant varieties such as Cavendish were regarded as the most effective method to handling Foc. However, recent studies showed that Cavendish is the most susceptible banana variety to Foc TR4 (Dita et al., 2018). Therefore, another approach is needed due to the rapid spread of Foc (O'Neill et al., 2016).

Suppressive soil can be used as an alternative to suppress Foc because it can reduce disease symptoms over time (Schlatter et al., 2017). Soil suppression utilizes the potential of native soil microbes to suppress pathogens (Mazzola and Freilich, 2017) and the complex relationship of a combination of either biotic or abiotic factors (Weller et al., 2002). However, microbial composition and functional activity are essential factors in suppressive soil formation (Schlatter et al., 2017).

Plant growth-promoting rhizobacteria (PGPR) are key to changing the soil ecosystem since the interactions between plant roots and soil microbes impact the plant health, production quantity, and soil quality (Meghvansi and Varma, 2016). PGPR is also considered a promising agent to reduce disease occurrence and increase commercial crop production (Beibei et al., 2016) through a direct and indirect mechanism (Goswami et al., 2016).

According to Beneduzi et al. (2012), PGPR is very diverse and can become biocontrol agents that utilize the antagonism to soil-borne pathogen through the production of siderophores and antibiotics. Although the ability of siderophore for each bacteria is different in iron uptake, in general, the affinity of siderophore bacteria is higher than fungi. Thus, it could suppress pathogenic fungi (Saharan and Nehra, 2011).

PGPR produces phytohormones, nitrogen-fixing, and solubilizes phosphorus to promote plant growth (Tabassum et al., 2017). PGPR can create various phytohormones such as auxins, gibberellins, cytokinins, ethylene, and abscisic acid to mediate plant cell enlargement, division, and extension in symbiotics or non-symbiotics roots (Goswami et al., 2016). In addition, PGPR can reduce the need for chemical fertilizers such as nitrogen and phosphorus by the production of phytohormones (Amara et al., 2015).

In general, PGPR contributes to the mechanism of suppressive soils through competition, antibiosis, parasitism, and induced plant resistance to pathogens (Janvier et al., 2007). Other keys to developing soil suppressive including soil properties (Meghvansi and Varma, 2016), soil microbes activity (Bruggen and Semenov, 2000), microbial composition and diversity (Garbeva et al., 2006), and agronomic management (Larkin and Honeycutt, 2005).

However, suppressive soil mechanisms remain unclear due to the high complexity in suppressive soil formation (Cha et al., 2016), and each pathogen has different suppressive soil characteristics (Janvier et al., 2007). Due to the high complexity and specificity, the use of disease-suppressive soils will become an effective solution if specifically based on host, pathogen, microbiome, and environment (Allard and Micallef, 2019). The more understanding of complex microbial interactions, the greater chances to develop specific grower practices based on soil suppressiveness (Schlatter et al., 2017).

Therefore, a metagenomic analysis was carried out to predict microbial composition and interactions between microbes (Quince et al., 2017) to understand soil suppressive against Foc. Also, the key taxa in suppressive soil against Foc could be predicted by metagenomic analysis (Expósito et al., 2017). This study aimed to analyze the abundance and diversity of soil microbes and predict the key taxa that are supposed to play a pivotal role in the soil suppressiveness formation against *Fusarium oxysporum* f.sp cubense. Moreover, the key species' roles in soil suppressiveness were scrutinized by analyzing the microbes' co-occurrence network and functional prediction.

2. Materials and methods

2.1. Soil sampling

Soil samples were collected according to Shen et al. (2015) with modification. On the dry season in June 2019, duplicates of healthy and infected banana trees of the same age were selected randomly from PT. Perkebunan Nusantara VIII Parakansalak, Sukabumi, Indonesia. Soil samples were collected by making a composite soil from each soil sampling site. The composite soil was made by thoroughly homogenizing triplicate soil samples from each soil sampling site with a depth of 20 cm. The collected soil composites from each site were stored in a sterile plastic bag and kept on an icebox during transport to the lab. Soil samples were stored at -80 °C for further analysis. The coordinate of the soil sampling site and the mean of physical and chemical conditions are shown in Table 1.

2.2. DNA extraction and sequencing

Total soil microbes DNA were isolated using ZymoBIOMICS™ DNA Miniprep Kit (United States of America). A total of 250 mg soil samples were put into a tube containing 500 mg glass bead and 750 µl ZymoBIOMICS™ DNA Miniprep Kit lysis buffer, and then mechanical lysis was carried out using Tehtnica™ Millmix20 (United Kingdom) at full speed for 20 min. Lysed soil samples were then isolated according to the manufacturer's protocol. Pooled total DNA was carried out from three technical replication for each soil sample to increase the yield of DNA isolate (Koo et al., 2018). Total DNA was sent to Novogene Singapore for shotgun-sequencing with Illumina NovaSeq™ 6000 150 paired-end.

2.3. Data analysis

Raw data obtained from sequencing is processed by bioinformatics, including pre-processing and processing analysis in High-Performance Computing. The raw data are available at NCBI BioProject under accession number: PRJNA670586. Direct link to the deposited data https://www.ncbi.nlm.nih.gov/Traces/study/?acc=PRJNA670586&o=acc_s%3Aa.

The pre-processing was carried out to quality control the DNA sequences, while the processing analysis is carried out to obtain the predictions of microbial composition, interaction, and function. Raw data received from the sequencing process has been filtered from N content >10%, primer sequences, low-quality sequences, and adapter sequences (Forward: 5′-AATGATACGGCGACCACCGAGATCTACACTCTTTCCCTACACGACGCTCTTCCGATCT-3′ Reverse: 5′-GATCGGAAGAGCACACGTCTGAACTCCAG TCACATCACGATCTCGTATGCCGTCTTCTGCTTG-3′) as shown in Table 2.

The quality control DNA sequences were carried out by FASTQC Graphical User Interface ver.0.11.5 (Andrews, 2010) and visualized with MultiQC to summarize multiple reports in the single plot, which can be shared and opened in the web browser (Ewels et al., 2016). MultiQC was performed in the Unix System by installed it through Anaconda Environment by type conda install -c bioconda -c conda-forge multiqc. The quality control plot is generated by type multiqc in the report analysis directory.

The processing analysis was started by de-novo assembly using MEGAHIT ver.1.2.9 (Li et al., 2015), 20 CPU, and 61 GB RAM. The metagenome assembly generated by type megahit -1 raw_data/HA_1.fq.gz -2 raw_data/HA_2.fq.gz -o HA_result. The output of the metagenome assembly called final contigs was in the FASTA file used for downstream bioinformatics analysis. The final contigs were evaluated using BBMap downloaded through https://downloads.sourceforge.net/project/bbmap/BBMap_35.34.tar.gz using the wget command. The evaluation was

Table 1. The coordinate of soil sampling site and the mean of abiotic condition.

Soil type	Coordinate	Mean			
		pH	Temperature (°C)	Humidity (%)	Light intensity (cd)
Healthy	6°49′43.0″S106°44′37.1″E 6°49′43.0″ S106°44′36.9″ E	4.63	24.8	0.5	515
Infected	6°49′41.4″S106°44′38.2″E 6°49′41.4″ S106°44′38.2″ E	4.55	25	0.5	555

Table 2. Raw data of suppressive and conducive sequences. Raw data has filtered from N content >10%, primer, low-quality sequences, and adapter sequences.

Sample	Raw reads	Clean reads	Effectivity (%)	GC content (%)
Suppressive A read1	41,452,346	41,378,758	99.82	63.72
Suppressive A read2	41,452,346	41,378,758	99.82	63.72
Suppressive B read1	34,140,203	34,096,509	99.87	63.31
Suppressive B read2	34,140,203	34,096,509	99.87	63.31
Conducive A read1	48,657,900	48,579,078	99.84	63.62
Conducive A read2	48,657,900	48,579,078	99.84	63.62
Conducive B read1	46,637,257	46,573,835	99.86	63.31
Conducive B read2	46,637,257	46,573,835	99.86	63.31

performed by bbmap/bbwarp.sh and bbmap/pileup.sh command (Bushnell, 2014).

The final contigs from metagenome assembly were then aligned by DIAMOND ver.0.9.24.125 using NCBI-nr as a database containing RefSeq, UniPortKB/Swiss-Prot, PDB, and PRF non-redundant CDS. The database was downloaded using the wget ftp://ftp.ncbi.nlm.nih.gov/blast//db/FASTA/nr.gz command. The downloaded NCBI-nr was then build up for alignment database using diamond makedb –in nr.gz -d nr –masking 0 command line. The alignment was performed using the diamond blastx command, which is 20,000 times faster than standard BLASTX tools. The DIAMOND software only considered the alignments with the expected value of ≤0.001 (Buchfink et al., 2014). The output of DIAMOND alignment was Diamond Archive Alignment (DAA) file used for taxonomic, co-occurrence network, and functional analysis using MEGAN6 software. The full command line that was used for the analysis attached in the Supplementary Information 1.

In the MEGAN6 software, the taxonomic and functional analysis started by indexing the DAA file using the Meganizer option by mapped the file into the Megan-map-Oct2019-ue.db. The Megan-map was downloaded from https://software-ab.informatik.uni-tuebingen.de/download/megan6/welcome.html contains NCBI taxonomic, KEGG, COG, InterPro2GO, and SEED. By default, MEGAN6 used the naive LCA algorithm for taxonomic binning. The LCA algorithm was assigned each read to the lowest common ancestor node that conceptually provides fast and sensitive taxonomic binning (Huson et al., 2016). Figure 1 showed the analysis overview in this study.

2.4. Data visualization

The relative abundance of microbes was visualized using STAMP to get a statistical overview of the data (Parks et al., 2014). While using STAMP, the data tables generated by MEGAN6 used as input data. The data tables were created by clicked file > export > STAMP format to get the.spf file used for visualization in the STAMP software. The STAMP can visualize the data into the PCA plot, heatmap plot, bar plot, box plot, post-hoc plot, and scatter plot. In this study, the relative abundance of the microbe was visualized into the scatter and box plots. In the STAMP, the data were visualized by clicked the file > load data and then inputted the.spf file generated by MEGAN6 and the metadata.

While the rarefaction curve, alpha diversity, PCoA plot, and co-occurrence network plot were carried out by MEGAN6 (Huson et al., 2016). The rarefaction curve was generated by collapsed the data into the

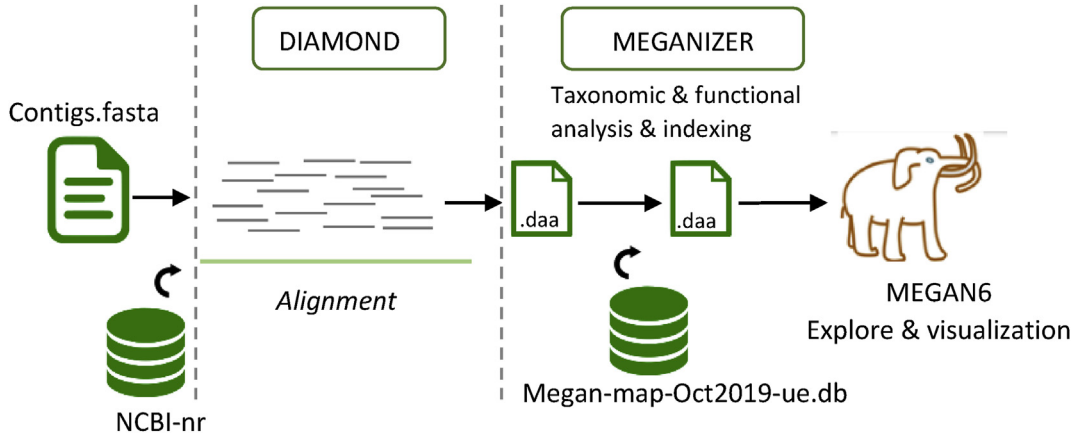

Figure 1. An overview of data analysis was performed in this study. The picture showed the final contigs from the de-novo assembly were aligned with DIAMOND using NCBI-nr as a database. The output data from DIAMOND were inputted into the MEGAN to explore and visualization the data.

species trees and then clicked the rarefaction icon. While the alpha diversity was created by clicked the Shannon-Weaver index in the Option menu of MEGAN6 after collapsed the data into the species trees. The co-occurrence network was also generated after the trees collapsed into the species. In the MEGAN6, the Spearman's Index, Pearson's Index, and Jaccard's Index can be used to generate the co-occurrence networks. In this study, the co-occurrence network generated using the Jaccard's Index due to insensitivity to co-absent sites may be a more appropriate metric to quantify the correlation in microbial systems (Mainali et al., 2017). The co-occurrence networks generated co-presence and co-absence of the microbes. The co-presence indicated a positive relationship, such as mutualism symbiosis, while the co-absence indicated a negative relationship such as competence and parasitism symbiosis.

3. Results and discussion

3.1. Sequences quality control and metagenome assembly

The results of the sequence quality analysis showed all samples have a Phred score above 30. Therefore, the accuracy rate of the sequencing process is approximately 99.9%, with a probability of error of 1/1000 of the sequence (Illumina, 2011). The results of the quality control showed in Supplementary Information Figure S1.

The de-novo metagenome assembly was carried out after data quality control. The approach used for the de-novo metagenome assembly is the succinct de Bruijn graph (sdBg) by splitting the sequences from short k-mer to long k-mer. In the overlapping area of k-mer, a new node will be formed to produce the assembly construct. The use of short k-mer sizes in chart formation can help overcome genomes with low abundance (Quince et al., 2017).

The results of the metagenome assembly showed the N50 value was in the hundreds. N50 is used as a parameter for assembly quality (Ayling et al., 2019). The low N50 value is due to the complex soil sample assembly (Méndez-García et al., 2018). Li et al. (2015) also obtained N50 values from soil samples with hundreds of values. The metagenome assembly results showed in Table 3.

According to Méndez-García et al. (2018), the N50 value rarely correlates with the de-novo metagenome assembly's actual quality. It becomes meaningless to construct many sequences with varying degrees of abundance as in metagenomic samples. Therefore, the mapping back approach was carried out to measure the quality of the metagenome assembly. The higher mapping back value indicates the high assembly quality—the value of mapping back above 90%, as shown in Table 4. According to Table 4, the results of the sequence quality analysis and de-novo metagenome assembly evaluation indicated that the sequences have good quality and can be used for further analysis.

3.2. The diversity and abundance of microbes

The alpha diversity showed that suppressive soils had higher microbial diversity than conducive soils based on the Shannon and Simpson index. The high alpha diversity index in suppressive soil indicates a higher possibility of interaction between soil microbes and pathogens, which have implications for suppressive soils (Expósito et al., 2017). Mazurier et al. (2009) reported that soil suppression against Foc was associated with high microbial diversity. The results of the alpha diversity analysis showed in Supplementary Information Table S1. While the rarefaction curve is shown in Supplementary Information Figure S2.

Furthermore, beta diversity analysis based on the Bray-Curtis dissimilarity and Weighted Uniform Unifrac did not show any groupings in suppressive soil samples and neither conducive soil samples (Figure 2). The Bray-Curtis approach is based on the species abundance in a community; thus, communities with an abundance range do not form in one group (Chao et al., 2005), while Weighted Uniform Unifrac is based on sequence space and species abundance (Lozupone et al., 2010).

Biplot lines on the beta diversity plots showed a species that have the most influence on PCoA formation, such as *Ktedonobacter racemifer, Candidatus Koribacter versatilis,* and *Rhodopseudomonas palustris*. Besides, biplot lines showed *Rhodopseudomonas palustris* was a higher abundance in suppressive soils. *Rhodopseudomas palustris* is one of the PGPR that can promote plant growth and increase microbes diversity in the soil (Wong et al., 2014).

The comparison of microbes abundance in this study was carried out from two groups of soil samples from phylum to species taxa level. The abundance analysis at the phylum level showed Proteobacteria and Actinobacteria were higher in the suppressive than conducive soils. Proteobacteria have large morphological, physiological, and metabolic diversity. These bacteria have a critical role in the carbon, nitrogen, and sulfur cycles (Kersters et al., 2006). Actinobacteria play an important part in replacing the carbon cycle, providing nutrients for the soil, forming humus, and producing various secondary metabolites such as antibiotics (Anandan and Dharumadurai, 2016). The abundance of microbes at the phylum level showed in Figure 3.

The phylum of Acidobacteria showed higher in conducive than suppressive soils. Acidobacteria can use nitrite as a source of N, provide soil micro-macro nutrients, soil acidity, express various active transporters, and produce exopolysaccharides (Kielak et al., 2016). However, just a little physiological information has been found on Acidobacteria because they are challenging to grow in the laboratory (Ward et al., 2009).

The abundance analysis at the class level showed Acidobacteria, Alphaproteobacteria, Deltaproteobacteria, and Betaproteobacteria as the dominant bacteria found in suppressive and conducive soil. However, abundance analysis showed Betaproteobacteria had consistently higher in suppressive soils. The bacteria included in the Betaproteobacteria play a prominent role in the nitrification process; thus, it is needed for the sustainability of agricultural land (Wolińska, 2019). The abundance of microbes at the class level showed Figure 4.

The abundance at the Order level showed Rhizobiales, Burkholderiales, and Streptosporangiales were found higher in suppressive soils, while Ktedonobacterales and Myxococcales were higher in conducive soils. Rhizobiales are soil microbiota that can interact with host plants (Garrido-Oter et al., 2018), support the formation of symbiosis to produce auxins, vitamins, nitrogen fixation, and protect the plants against stress (Erlacher et al. 2015). In addition, Burkholderiales can increase

Table 3. The results of the de-novo metagenome assembly. The data showed a low of N50 due to the complex of soil sample assembly.

Output	Suppressive A	Suppressive B	Conducive A	Conducive B
Reads	82,904,692	68,280,406	97,315,800	93,274,514
Contigs	1,420,651	1,060,803	1,720,036	1,867,285
Total (bp)	750,909,979	536,895,957	932,838,956	1,075,841,203
Min (bp)	200	200	200	200
Max (bp)	37,580	20,110	41,582	78,024
Average (bp)	528	506	542	576
N50 (bp)	521	494	531	571

Table 4. The results of mapping back analysis of suppressive and conducive soils in percent. The more excellent value in the mapping back showed a high quality of de-novo metagenome assembly.

Sample	Suppressive A	Suppressive B	Conducive A	Conducive B
Percent scaffolds with any coverage	99.92	99.93	99.91	99.95
Percent of reference bases covered	98.80	98.73	98.83	99.13
Average coverage	4.07	3.69	4.25	4.00

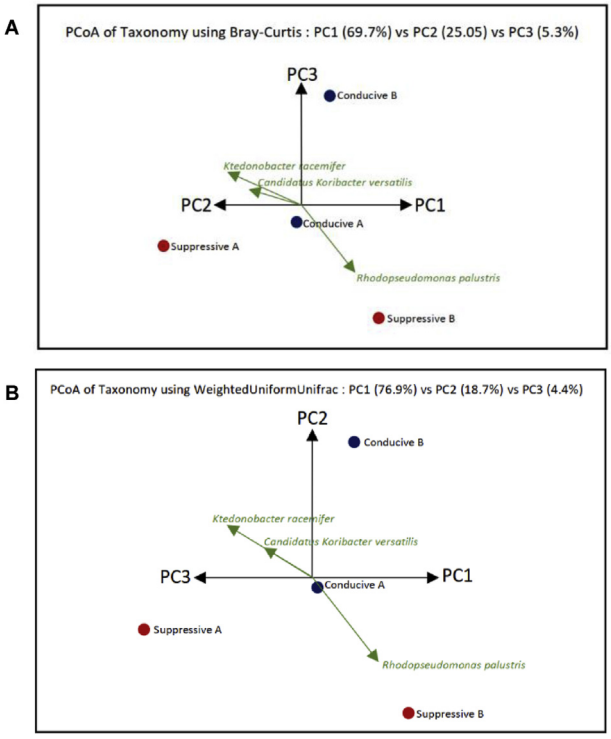

Figure 2. Beta diversity in suppressive and conducive soils (A) based on Bray-Curtis dissimilarity, (B) based on Weighted Uniform Unifrac showed no groupings among two groups of soil samples. The biplot line in the PCoA showed a species that have a significant influence on the PCoA formation.

microbes' abundance around plant roots and has beneficial interactions with plants (Aguirre-Von-Wobeser et al. 2018).

The abundance analysis at the family level showed *Acidobacteriaceae* and *Ktedonobacteraceae* were higher in the conducive soils, while *Bradyrhizobiaceae* and *Methylobacteraceae* were higher in the suppressive soils. The *Acidobacteriaceae* group is known challenging to be isolated and has low cell growth ability; thus, its physiological function is not widely known (Campbell, 2014). However, based on the genome analysis of the Acidobacteria, they could survive in a polluted and extreme environment such as an environment with low acid levels (Ward et al., 2009). The *Ktedonobacteraceae* has many genera that cannot be cultured; thus, its physiological function is not widely known (Yabe et al., 2017). The functional analysis of *Ktedonobacteraceae* using KEGG showed it could degrade xenobiotic compounds in the soil (de Vries et al., 2015). The *Methylobacteraceae* known can induce plant root and leaf nodules (Kelly et al., 2014), while *Bradyrhizobiaceae* known to have an essential role in nitrogen fixation (Lucia et al., 2014).

The abundance analysis at the species level showed *Candidatus Koribacter versatilis* and *Ktedonobacter racemifer* were higher in the conducive soils. *C. Koribacter versatilis* belongs to the phylum of Acidobacteria, which can live in a polluted environment (Ward et al., 2009) and an environment with low acid levels (Sait et al., 2006). Besides, *K. racemifer* can live in microaerophilic conditions (Chang et al., 2011) and can survive in poor nutritional conditions (Barton et al., 2014). Suppressive soils showed a higher abundance of *Rhodopseudomonas palustris* and *Methylobacterium nodulans*. *R. palustris* has a high metabolic rate, can perform nitrogen fixation (Larimer et al., 2004), increase plant growth, stress resistance, and improve soil microbial composition (Wong et al., 2014).

In recent years, *R. Palustris* as photosynthetic bacteria have been used widely in agriculture, but the culture method and application in the banana plantation still lack information. Several works reported that it could promote plant growth by producing indole-3-acetic acid and 5-aminolevulinic acid (Su et al., 2017), encourage resistance stress by producing peroxidase, and significantly affect rice rhizosphere bacterial communities (Luo et al., 2019). The culture method of *R. palustris* has been investigated using 39.41 ml/L corn steep liquor and 32.25 g/L molasses at temperature 37.9 °C, pH 7.0, and 30% DO (Lo et al., 2020). Other work also reported that the use of landfill leachate with 16.0 g/L total organic carbon and 1.1 g/L total nitrogen could use as medium growth of *R. palustris* (Wang et al., 2018).

Furthermore, *M. nodulans* were also reported as promising growth-promoting bacteria (Kelly et al., 2014), but still lack information. *M. nodulans* is the only nodulating bacterium in the genus *Methylobacterium* due to the presence of the NodA gene (Sy et al., 2001). Other work reported that it has a symbiotic association with plants and can grow on C_1 compounds such as methanol, formate, and formaldehyde (Jourand et al., 2004). Microbes abundance from order to species level showed in Figure 5.

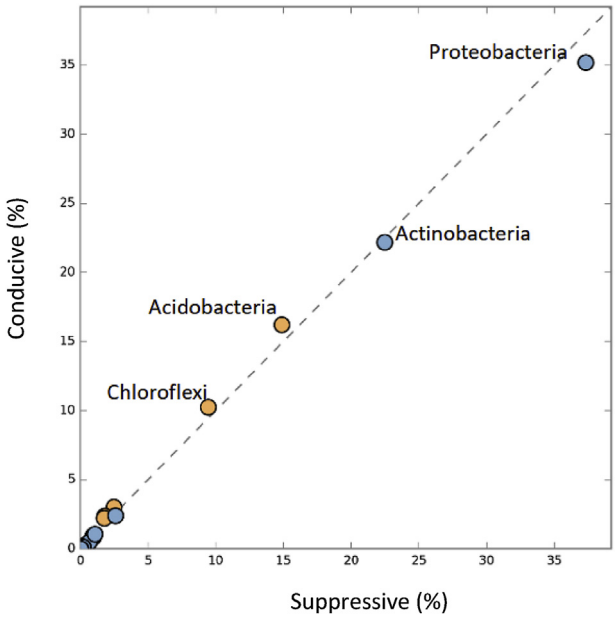

Figure 3. Microbial abundance at the phylum level in suppressive and conducive soils. Microbes with a higher abundance in suppressive soils are shown in blue, while on conducive soils are shown in orange. This plot showed Proteobacteria and Actinobacteria were higher in suppressive than conducive soils.

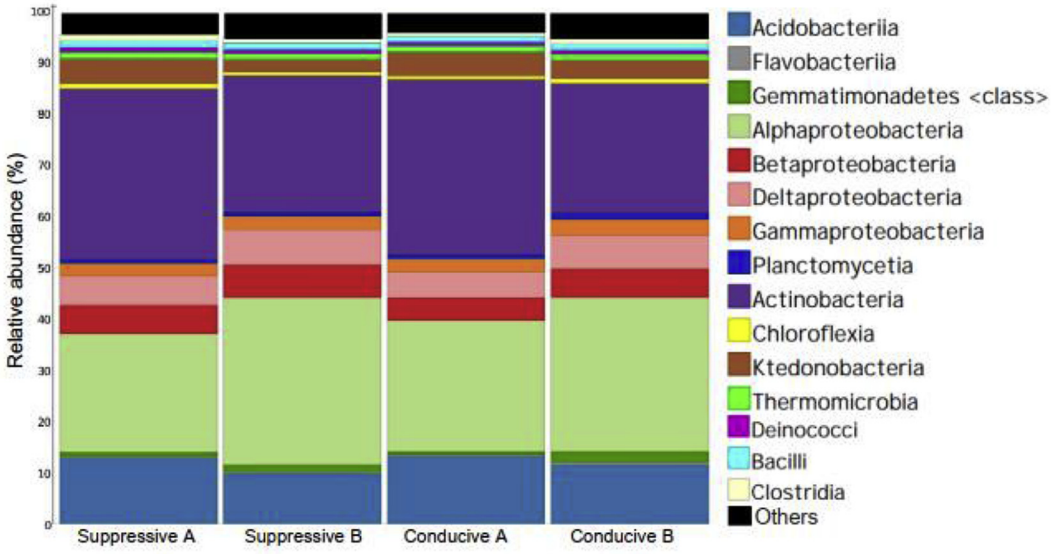

Figure 4. Microbial abundance at the class level showed a consistently higher abundance of Betaproteobacteria in the suppressive than conducive soils showed by a red color. The bacteria in the Betaproteobacteria group known to have a prominent role in the sustainability of agricultural land due to nitrogen nitrification capability.

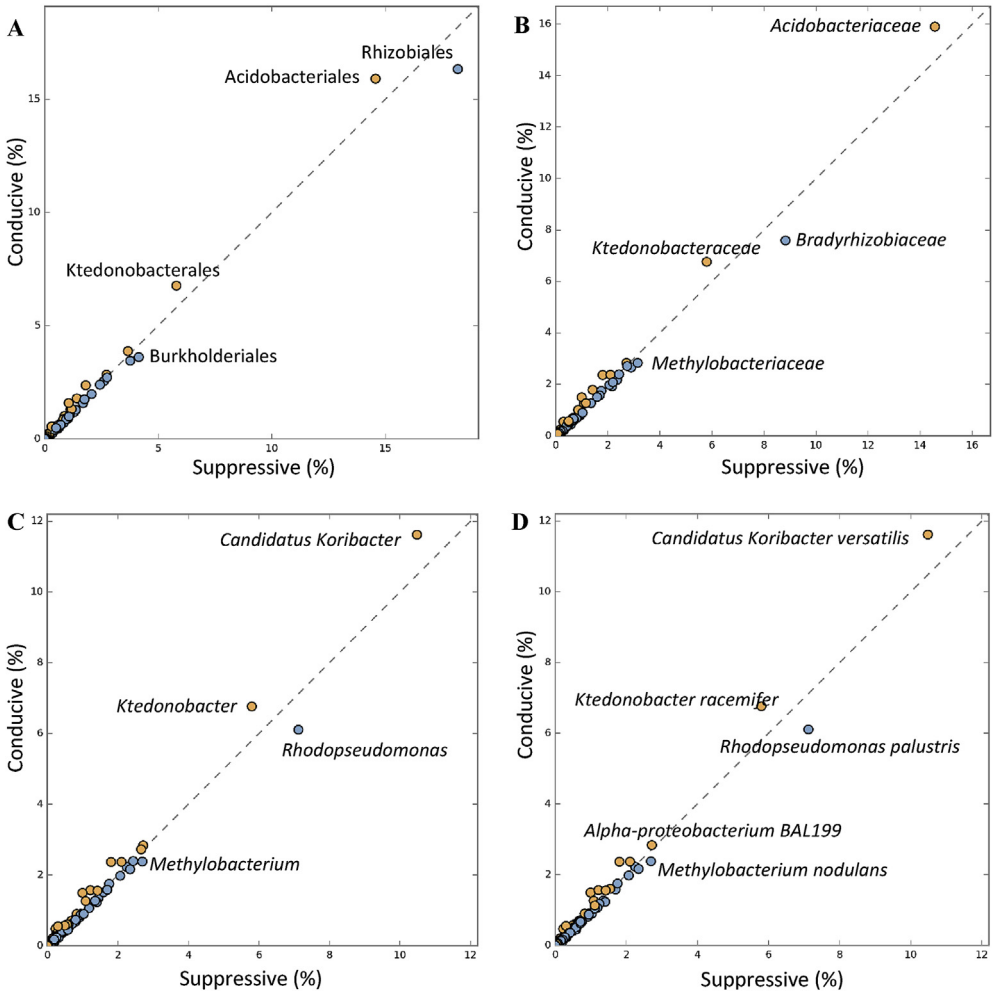

Figure 5. The microbes abundance from order to species level in suppressive and conducive soils. (A) Ordo, (B) Family, (C) Genus, (D) Species. Microbes with a higher abundance in suppressive soil are shown in blue, while on conducive soil are shown in orange. This plot showed the species *Rhodopseudomonas palustris* and *Methylobacterium* nodulans as dominant species with PGPR activity in the soil.

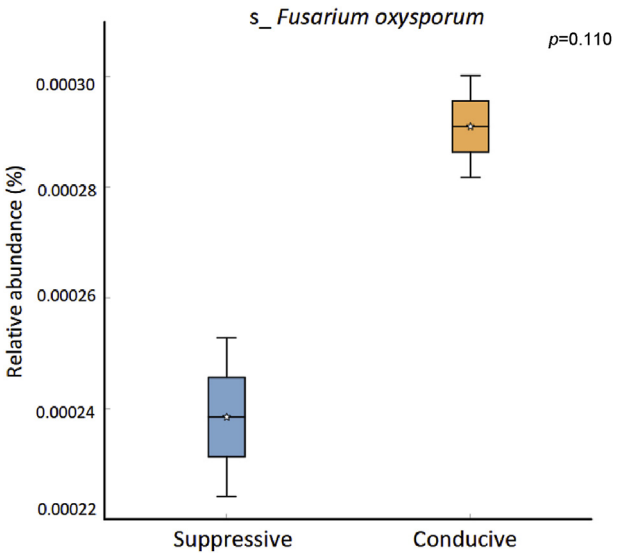

Figure 6. The abundance of *Fusarium oxysporum* showed lower in the suppressive than conducive soils. It assumed that the high abundance of PGPR in the suppressive soils could suppress *Fusarium oxysporum* and help perform soil suppression against the pathogen.

This study showed the abundance of PGPR was found higher in the suppressive soils than the conducive soils. Thus, it can be assumed that PGPR plays a role in Foc growth suppressing. PGPR can increase plant growth by providing nutrients and protecting plants from biotic and abiotic stress (Goswami et al., 2016). Thus, PGPR can improve the quality and diversity of soil microbes (Ren et al., 2020). This study found an abundance of *Fusarium oxysporum* is lower in suppressive soils, as shown in Figure 6.

3.3. Co-occurrence networks

The co-occurrence network analysis was carried out to identify ecological relationships, both positive and negative interactions (Widder et al., 2014). This study found two groups of positive interaction in suppressive soil contain 37 species. The positive interactions can occur because of a mutually beneficial mutualistic relationship between taxa (Suweis et al., 2013). This analysis found *Pseudomonas* sp., *Burkholderia* sp., and *Streptomyces* in the suppressive soil co-occurrence network shown in Figure 7.

The co-occurrence network analysis in the conducive soils found that 42 species were performing in the interaction. The co-occurrence analysis of conducive soils did not found *Pseudomonas* and *Burkholderia* similar to in the suppressive soils. In the conducive soils, *Bacillus* and more *Streptomyces* in the interaction were not identical as in the suppressive soils. The co-occurrence network of conducive soils showed in Figure 8.

The presence of *Pseudomonas, Burkholderia, Streptomyces*, and *Bacillus* in the co-occurrence analysis is assumed that bacteria respond against Foc actively. *Pseudomonas, Burkholderia,* and *Bacillus* are known as PGPR that can solubilize phosphate and fix nitrogen (Vessey, 2003). Besides, *Streptomyces* is known able to control nematode *Meloidogyne incognita* (Ruanpanun et al., 2010) and produce many secondary metabolites such as volatile organic compounds (VOCs), which can inhibit the growth of fungal hyphae the pathogenic fungus *Rhizoctonia solani* (Cordovez et al., 2015). *Pseudomonas* has been widely studied for its ability to suppress *Fusarium* and become a promising bio-control candidate (Mazurier et al., 2009). Table 5 shown the function of assumed bacteria from co-occurrence analysis that plays a role against Foc.

The abundance analysis of assumed bacteria from co-occurrence analysis was carried out to see its differences in the suppressive and conducive soils. The abundance analysis showed a higher abundance of *Bacillus* in the suppressive than the conducive soils, but it was not found in the suppressive soil co-occurrence network analysis. Besides, the abundance of *Streptomyces* and *Pseudomonas* was not different in both soil samples. But, *Pseudomonas* was found in the suppressive soil co-occurrence network analysis. It may be assumed *Pseudomonas* is an important species in suppressive soils. The abundance of *Burkholderia* showed differences in both soil samples. Thus it is thought that *Burkholderia* and *Pseudomonas* as key species in the formation of suppressive soils against Foc. The use of *Burkholderia* and *Pseudomonas* can promote plant growth and reduce disease in valuable agricultural commodities (Tabassum et al., 2017). The abundance of *Bacillus, Streptomyces*, *Burkholderia*, and *Pseudomonas* showed in Figure 9.

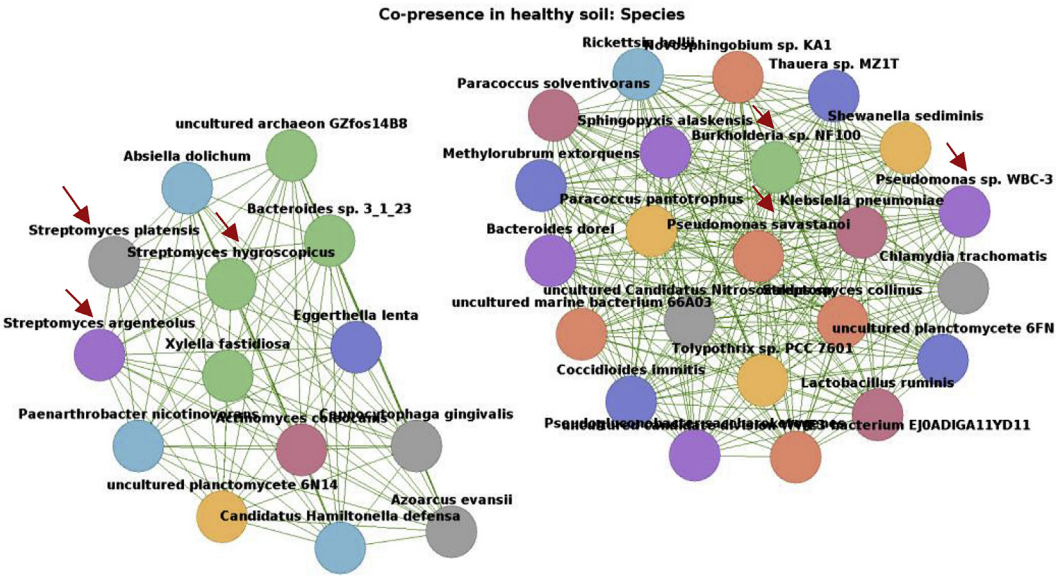

Figure 7. Two groups of positive interaction in the co-occurrence network analysis in the suppressive soils. The red arrow showed the presence of *Burkholderia, Pseudomonas,* and *Streptomyces* are assumed to have an implication for the formation of the suppressive soils against Foc.

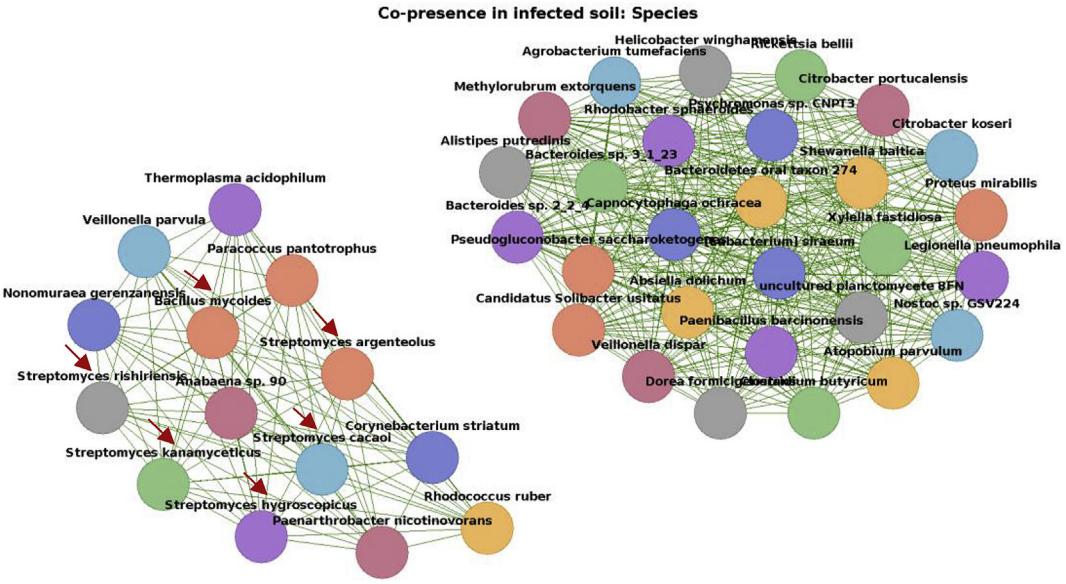

Figure 8. The co-occurrence analysis of conducive soils performing two groups of positive interactions similar to in the suppressive soils. In the conducive soils were not found *Pseudomonas* and *Burkholderia,* but *Bacillus* and more *Streptomyces* were identified in the interactions. The presence of *Streptomyces* and *Bacillus* showed by the red arrow.

Table 5. The function of microbes that found in the suppressive and conducive soils co-occurrence network analysis that assumed play a role in the suppressive soil formation.

Microbes	Functions	References
Streptomyces platensis	Producing platensymicin and platencin antibiotics broad-spectrum against gram-positive pathogens such as *Staphylococcus aureus*	(Smanski et al., 2009).
Streptomyces hygroscopicus	Producing rapamycin antibiotics that have antifungal activity and inhibits cell growth widely through the non-competitive mechanism	(Staunton and Wilkinson, 1999); (Schreiber et al., 2016).
Streptomyces argenteolus	Have an activity against plant pathogens through antagonistic mechanisms by producing antimicrobials	(Moon-cheol et al., 2009)
Pseudomonas sp.	Producing siderophore and phenazines to suppress Foc through competitive and antagonistic mechanisms	(Mazurier et al., 2009).
Burkholderia sp.	Have an antifungal activity such as *Burkholderia rinojensis, Burkholderia seminalis* TC3.4.2R3, *Burkholderia cepacia, Burkholderia gladioli, Burkholderia cenocepacia, Burkholderia ambifaria* able to degrade fusaric acid	(Abdel-aziz et al., 2020); (Diana et al., 2017); (Heydari and Misaghi, 1998); (Li et al., 2007); (Elshafie et al., 2012); (Rojas-rojas et al., 2018); (Simonetti et al., 2018)
Streptomyces kanamycetius	Producing kanamycin	(Basak and Majumdar, 1975).
Streptomyces rishiriensis	Producing coumermycin	(Li et al., 2002)
Streptomyces cacaoi	As an antifungal activity against *Fusarium*	(Janaki, 2017)
Bacillus mycoides	Inducing colonization of endophytic bacteria	(Yi et al., 2017)

3.4. Functional analysis of Burkholderia and Pseudomonas

The functional analysis of *Burkholderia* and *Pseudomonas* was carried out to understand the role of both bacteria in soil suppressiveness formation. Based on the *Burkholderia* functional analysis, two zinc/manganese transport systems were higher in the suppressive than conducive soils. Meanwhile, the *Pseudomonas* functional analysis was found phosphate transport systems only present in the suppressive soils. The functional analysis of *Burkholderia* and *Pseudomonas* in the suppressive soils was shown in Figure 10, while the functional analysis for conducive soils analysis showed in Supplementary Information Figure S3.

According to KEGG, the zinc/manganese transport system is a part of prokaryotes ABC transporters that able to transport metallic cation, iron-siderophore, and vitamin B12 (Kanehisa and Goto, 2000; Kanehisa et al., 2019; Kanehisa, 2019). Its system is encoded by ZnuABC that has a high affinity to uptake metals (Patzer and Hantke, 1998). Some PGPR are able to release iron-chelating siderophore to help plant uptake several metals such as zinc, iron, and copper (Kumar et al., 2019). The use of siderophore able to suppress phytopathogens by sequestering iron in the rhizosphere (Ali et al., 2020).

According to Yu et al. (2011), the siderophore-producing bacterium able to control fusarium wilt and promote plant growth by the

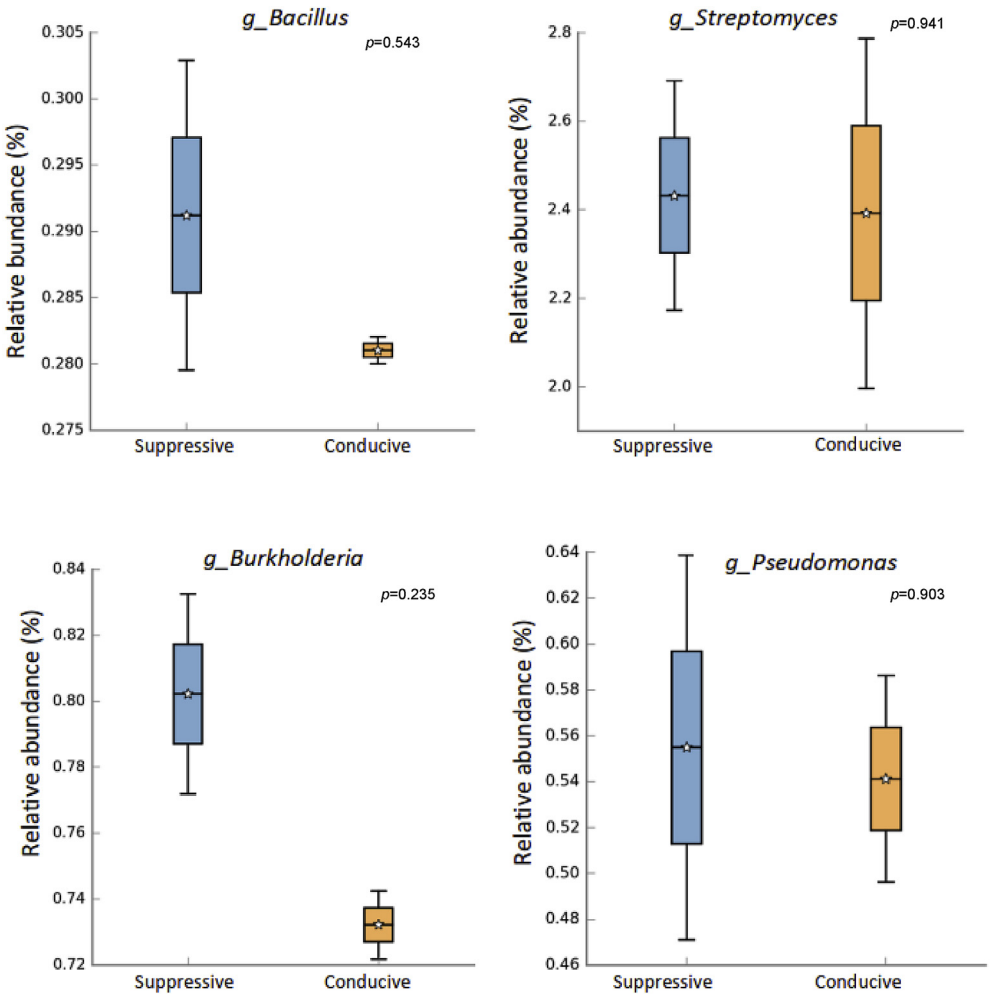

Figure 9. The abundance of *Bacillus, Streptomyces, Burkholderia*, and *Pseudomonas* in the suppressive soils showed in blue, while in conducive soils showed in orange. *Burkholderia* and *Pseudomonas* are assumed to be key species to perform suppressive soil against Foc based on co-occurrence network analysis and the abundance analysis in this plot.

antagonistic mechanism. The study conducted by Mazurier et al. (2009) showed the use of siderophore to inhibit *Fusarium oxysporum* growth in banana fusarium wilt disease. Therefore, this study assumed that the higher abundance of pathway zinc/manganese transport system in suppressive soil by *Burkholderia* helps plants uptake more nutrients for their growth and inhibit proliferation of Foc. Besides, *Burkholderia* is also known to have a high ability to solubilize inorganic phosphate (Goswami et al., 2016).

The use of *Burkholderia* to control *Fusarium* wilt banana has been reported to strongly inhibit the growth of Foc mycelial up to 44.4 % in Potato Dextrose Agar and 40% under greenhouse conditions (Ho et al., 2014). It also can produce antifungal metabolite phenazine-1-carboxylic acid (PCA). Experiments showed that the application of $\geq$5 μg/ml of PCA could control *Fusarium* wilt and promote banana growth efficiently (Xu et al., 2020). Other work also reported that *Burkholderia* could increase the activity of pathogenesis-related protein against *Fusarium* wilt under greenhouse conditions (Fishal et al., 2010).

Furthermore, this study found two phosphate transport systems in suppressive soils, which are phosphate transport system permease protein and substrate-binding protein. According to KEGG, the phosphate transport system permease protein is part of the prokaryotic ABC transporter pathway. While the phosphate transport system substrate-binding protein is part of ABC transporters and Two-component system pathway (Kanehisa and Goto, 2000; Kanehisa et al., 2019; Kanehisa, 2019). The *pst* operon encodes those transport systems to uptake insoluble inorganic phosphate to convert it into solubilize phosphate (Nikata et al., 1996).

Phosphate is an essential nutrient after nitrogen for a plant, but the plant can only uptake solubilize phosphate (Goswami et al., 2016). Therefore, plants need Phosphate Solubilize Bacteria (PSB), such as *Pseudomonas,* known to have a high ability to solubilize inorganic phosphates (Illmer and Schinner, 1992). Besides, PSB can increase phosphate uptake, crop yield (Rodríguez and Fraga, 1999), an alternative to chemical fertilizers, and promote plant growth (Oteino et al., 2015). This study was found *Pseudomonas* abundance, and phosphate transport systems were higher in suppressive soils. It is assumed that plants can uptake more nutrition provided by bacteria in suppressive soils.

This study is supported by other metagenomic work of banana root microbiome in Africa that found *Pseudomonas* was abundant in non-symptomatic bananas (Kaushal et al., 2020). *Pseudomonas* has been widely investigated as a promising biocontrol agent due to the ability for growth-promoting, phytopathogen suppression, and induces systemically induced resistance in plants (Tian et al., 2007). Thangavelu et al. (2003) reported that treatment of *Pseudomonas* in *Fusarium* wilt banana could increase several defense enzymes such as peroxidase, phenylalanine ammonia-lyase, chitinase, and β-1,3-glucanase activity after three days of inoculation. The accumulation of these enzymes is associated with increasing induced systemic resistance in plants

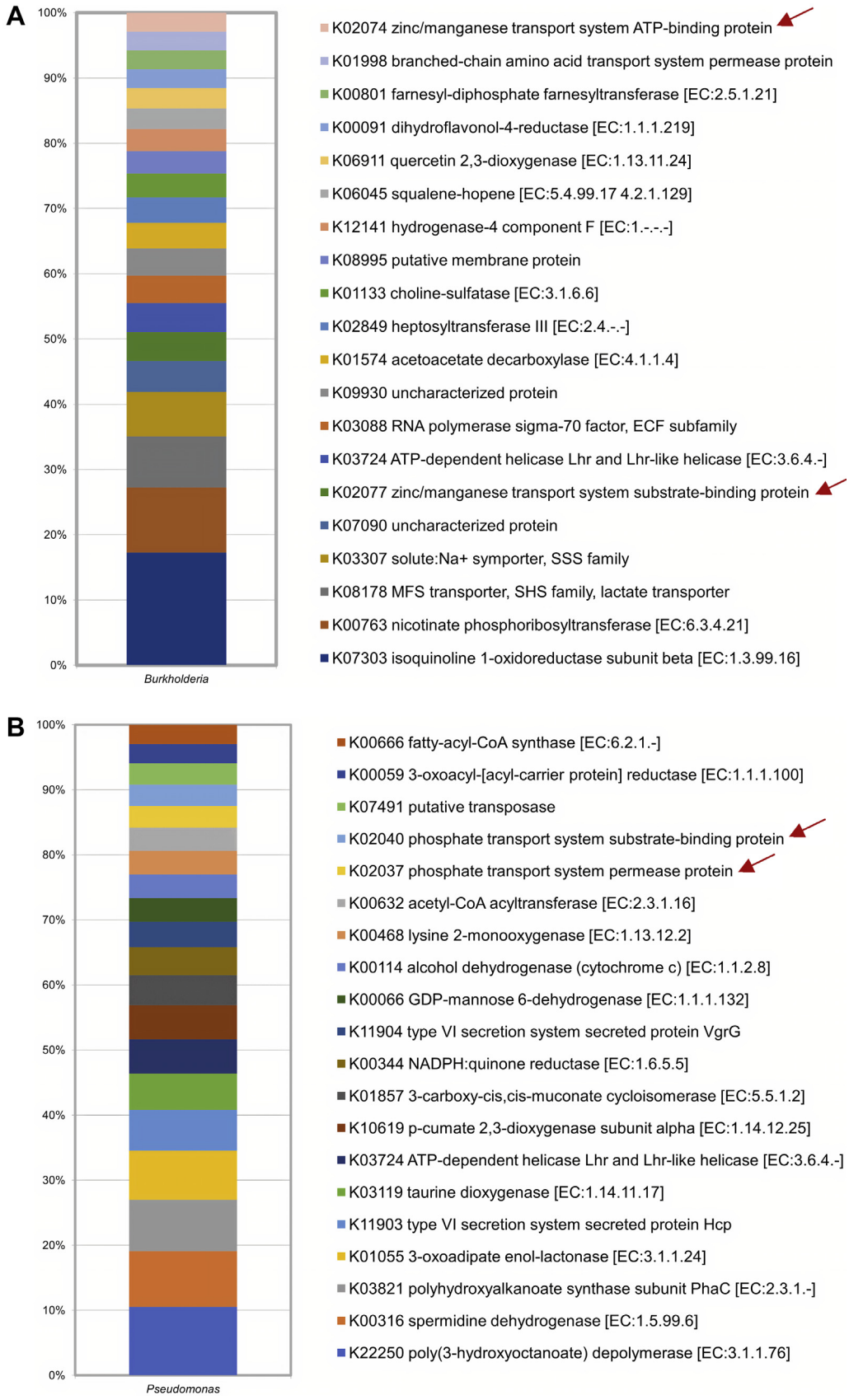

Figure 10. The functional analysis of *Burkholderia* (A) and *Pseudomonas* (B). Zinc/manganese transport system and phosphate transport systems showed by the red arrow are assumed to play a role in performing suppressive soil against Foc in this study.

(Lawton and Lamb, 1987). Bubici et al. (2019) also reported that *Fusarium* wilt banana had been controlled up to 79% using *Pseudomonas* spp. under field condition.

4. Conclusion

This study found PGPR may contribute to suppressing the presence of Foc in the soil. It was shown by a higher abundance of *Rhodopseudomonas palustris*, *Methylobacterium nodulans, Pseudomonas,* and *Burkholderia* in suppressive soils. This study also found that suppressive soils have a higher trend microbial diversity than conducive soils. The high microbial diversity in the soil can suppress pathogenic fungus through any mechanism such as antibiosis and competence. The co-occurrence analysis found that *Pseudomonas* and *Burkholderia* are assumed as key species in suppressive soils against Foc. The functional analysis found that zinc/manganese and phosphate transport systems responsible for synthesizing a siderophore and phosphate solubilization were higher in the suppressive soils. Overall, this study found nitrification bacteria, siderophore-producing bacterium, and phosphate solubilizes bacteria were promising biocontrol agents to suppress Foc.

Declarations

Author contribution statement

Lulu' Nisrina: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Yunus Effendi, Adi Pancoro: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

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Data availability statement

Data associated with this study has been deposited at the NCBI BioProject under the accession number PRJNA670586.

Competing interest statement

The authors declare no conflict of interest.

Additional information

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References

Abdel-aziz, M.M., Emam, T.M., Elsherbiny, E.A., 2020. Bioactivity of magnesium oxide nanoparticles synthesized from cell fi ltrate of endobacterium Burkholderia rinojensis against Fusarium oxysporum. Mater. Sci. Eng. C 109 (September 2019), 110617. Elsevier.

Aguirre-Von-Wobeser, E., et al., 2018. Enrichment of Verrucomicrobia, Actinobacteria and Burkholderiales drives selection of bacterial community from soil by maize roots in a traditional milpa agroecosystem. PloS One 13 (12), 1–18.

Ali, S., et al., 2020. Functional characterization of potential PGPR exhibiting broad-spectrum antifungal activity. Microbiol. Res. 232 (November 2019), 126389. Elsevier.

Allard, S.M., Micallef, S.A., 2019. The Plant Microbiome: Diversity, Dynamics, and Role in Food Safety, Safety and Practice for Organic Food. Elsevier Inc.

Amara, U., Khalid, R., Hayat, R., 2015. Soil Bacteria and Phytohormones for Sustainable Crop Production. Springer International Publishing Switzerland, pp. 87–103.

Anandan, R., Dharumadurai, D., 2016. An Introduction to Actinobacteria. Basic. Biotecnol. Appl. 3–38.

Andrews, S., 2010. FastQC: a quality control tool for high throughput sequence data. Available at: http://www.bioinformatics.babraham.ac.uk/projects/fastqc/.

Ashokkumar, K., et al., 2018. Nutritional value of banana (Musa spp.) cultivars and its future prospects: a review. Curr. Adv. Agricul. Sci. (An Int. J.) 10 (2), 73.

Ayling, M., Clark, M.D., Leggett, R.M., 2019. New approaches for metagenome assembly with short reads. Briefings Bioinf. (February), 1–11, 00.

Barton, A.H., et al., 2014. Microbial diversity in a Venezuelan orthoquartzite cave is dominated by the chloroflexi (class Ktedonobacterales) and thaumarchaeota group I. 1c. Front. Microbiol. 5 (November), 1–14.

Basak, K., Majumdar, S.K., 1975. Mineral nutrition of Streptomyces kanamyceticus for Kanamycin formation. Antimicrob. Agents Chemother. 8 (4), 391–395.

Beibei, W., et al., 2016. Bacillus amyloliquefaciens strain W19 can promote growth and yield and suppress Fusarium wilt in banana under greenhouse and field conditions. Pedosphere 26 (5), 733–744.

Beneduzi, A., Ambrosini, A., Passaglia, L.M.P., 2012. Plant growth-promoting rhizobacteria (PGPR): their potential as antagonists and biocontrol agents. Genet. Mol. Biol. 35 (4 SUPPL), 1044–1051.

Bubici, G., et al., 2019. Biological control agents against Fusarium wilt of banana. Front. Microbiol. 10 (April).

Buchfink, B., Xie, C., Huson, D.H., 2014. Fast and sensitive protein alignment using DIAMOND. Nat. Method 12 (1), 59–60.

Bushnell, Brian, 2014. BBMap: a fast, accurate, splice-aware aligner [online]. available at: https://sourceforge.net/projects/bbmap/.

Calberto, G., Staver, C., Siles, P., 2015. An assessment of global banana production and suitability under climate change scenarios. In: Elbehri, A. (Ed.), Climate Change and Food Systems: Global Assessments and Implications for Food Security and Trade. Food Agriculture Organization of the United Nations (FAO), Rome.

Campbell, B.J., 2014. The Family Acidobacteriaceae. The Prokaryotes 405–415.

Cha, J.Y., et al., 2016. Microbial and biochemical basis of a Fusarium wilt-suppressive soil. ISME J. 10 (1), 119–129.

Chang, Y., et al., 2011. Non-contiguous finished genome sequence and contextual data of the filamentous soil bacterium Ktedonobacter racemifer type strain (SOSP1-21). Stand. Genom. Sci. 5, 97–111.

Chao, A., et al., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8, 148–159.

Cordovez, V., et al., 2015. Diversity and functions of volatile organic compounds produced by Streptomyces from a disease-suppressive soil. Front. Microbiol. 6, 1–13.

de Vries, M., et al., 2015. Metagenomic analyses reveal no differences in genes involved in cellulose degradation under different tillage treatments. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 91 (7), 1–10.

Diana, F., Araújo, W.L., Eberlin, M.N., 2017. Potential of burkholderia seminalis TC3.4.2R3 as biocontrol agent against Fusarium oxysporum evaluated by mass spectrometry imaging', *American Society for mass spectrmetry*. J. Am. Soc. Mass Spectrom. 28 (5), 901–907.

Dita, M., et al., 2018. Fusarium wilt of banana: current knowledge on epidemiology and research needs toward sustainable disease management. Front. Plant Sci. 871 (October), 1–21.

Elshafie, H.S., et al., 2012. In vitro antifungal activity of burkholderia gladioli pv . agaricicola against some phytopathogenic fungi. Int. J. Mol. Sci. 13 (12), 16291–16302.

Erlacher, A., et al., 2015. Rhizobiales as functional and endosymbiontic members in the lichen symbiosis of Lobaria pulmonaria L. Front. Microbiol. 6, 1–9.

Ewels, P., et al., 2016. MultiQC: summarize analysis results for multiple tools and samples in a single report. Bioinformatics 32 (19), 3047–3048.

Expósito, R.G., et al., 2017. Current insights into the role of Rhizosphere bacteria in disease suppressive soils. Front. Microbiol. 8 (DEC), 1–12.

Garbeva, P., et al., 2006. Effect of above-ground plant species on soil microbial community structure and its impact on suppression of Rhizoctonia solani AG3. Environ. Microbiol. 8 (2), 233–246.

Garrido-Oter, R., et al., 2018. Modular traits of the Rhizobiales root microbiota and their evolutionary relationship with symbiotic rhizobia', cell host and microbe. Elsevier 24 (1), 155–167.e5.

Goswami, D., Thakker, J.N., Dhandhukia, P.C., 2016. Portraying mechanics of plant growth promoting rhizobacteria (PGPR): a review. Cogent Food Agricul. Cogent 2 (1).

Harrach, B.D., et al., 2013. The mutualistic fungus *Piriformospora indica* protects barley roots from a loss of antioxidant capacity caused by the necrotrophic pathogen *Fusarium culmorum*. Mol. Plant Microbe Interact. 26 (5), 599–605.

Hermanto, C., et al., 2011. Incidence and distribution of Fusarium wilt disease of banana in Indonesia. Acta Hortic. 897, 313–322.

Heydari, A., Misaghi, I.J., 1998. Biocontrol activity of Burkholderia cepacia against Rhizoctonia solani in herbicide-treated soils. Plant Soil 202 (1), 109–116.

Ho, Y.N., et al., 2014. In planta biocontrol of soil-borne Fusarium wilt of banana through a plant endophytic bacterium, Burkholderia cenocepacia 869T2. Plant Soil 387 (1–2), 295–306.

Huson, D.H., et al., 2016. MEGAN community edition - interactive exploration and analysis of large-scale microbiome sequencing data. PLoS Comput. Biol. 12 (6), 1–12.

Illmer, P., Schinner, F., 1992. Solubilization of inorganic phosphates by microorganisms isolated from forest soils. Soil Biol. Biochem. 24 (4), 389–395.

Illumina, 2011. Quality Scores for Next-Generation Sequencing: Assessing Sequencing Accuracy Using Phred Queality Scoring. Qual. Scores Next-gener. Sequen. 1–2.

Janaki, T., 2017. Biocontrol of Fusarium oxysporum in unsterilized soil by novel Streptomyces cacaoi subsp cacaoi [M20]. Int. J. Pharm. Pharmaceut. Sci. 9 (3), 78–83.

Janvier, C., et al., 2007. Soil health through soil disease suppression: which strategy from descriptors to indicators? Soil Biol. Biochem. 39 (1), 1–23.
Jourand, P., et al., 2004. Methylobacterium nodulans sp . nov ., for a group of aerobic , facultatively methylotrophic , legume root-nodule-forming and nitrogen-fixing bacteria. Int. J. Syst. Evol. Microbiol. 54, 2269–2273.
Kanehisa, M., 2019. Toward understanding the origin and evolution of cellular organisms. Protein Sci. 28 (August), 1947–1951.
Kanehisa, M., Goto, S., 2000. KEGG: Kyoto Encyclopedia of genes and genomes. Nucleic Acids Res. 28 (1), 27–30.
Kanehisa, M., et al., 2019. New approach for understanding genome variations in KEGG. Nucleic Acids Res. 47 (October 2018), 590–595. Oxford University Press.
Kaushal, M., Mahuku, G., Swennen, R., 2020. Metagenomic insights of the root colonizing microbiome associated with symptomatic and. Plants 9 (263), 1–18.
Kelly, D.P., Mcdonald, I.R., Wood, A.P., 2014. The family Methylobacteriaceae. The Prokaryotes 313–340.
Kersters, K., et al., 2006. Introduction to the Proteobacteria. The Prokaryotes 3–37.
Kielak, A.M., et al., 2016. The ecology of Acidobacteria: moving beyond genes and genomes. Front. Microbiol. 7 (May), 1–16.
Koo, H., et al., 2018. Metagenomic analysis of microbial community compositions and cold-responsive stress genes in selected antarctic lacustrine and soil ecosystems. Life 8 (3).
Kumar, A., et al., 2019. Recent advances of PGPR based approaches for stress tolerance in plants for sustainable agriculture. Biocatal. Agricul. Biotechnol. 20 (May), 101271. Elsevier Ltd.
Larimer, F.W., et al., 2004. Complete genome sequence of the metabolically versatile photosynthetic bacterium Rhodopseudomonas palustris. Nat. Biotechnol. 22 (1), 55–61.
Larkin, R.P., Honeycutt, C.W., 2005. Effects of different 3-year cropping systems on soil microbial communities and Rhizoctonia diseases of Potato. Ecol. Epidemiol. 96 (1), 68–79.
Lawton, M.A., Lamb, C.J., 1987. Transcriptional activation of plant defense genes by fungal elicitor, wounding, and infection. Mol. Cell Biol. 7 (1), 335–341.
Li, S., et al., 2002. Methyltransferase genes in Streptomyces rishiriensis: new coumermycin derivatives from gene-inactivation experiments. Microbiological 148, 3317–3326.
Li, X., Quan, C., Fan, S., 2007. Antifungal activity of a novel compound from Burkholderia cepacia against plant pathogenic fungi. Lett. Appl. Microbiol. 45 (5), 508–514.
Li, D., et al., 2015. MEGAHIT: an ultra-fast single-node solution for large and complex metagenomics assmebly via succinct de Bruijn graph. Bioinformatics 1–2.
Lo, K.J., Lee, S.K., Liu, C. Te, 2020. Development of a low-cost culture medium for the rapid production of plant growth-promoting Rhodopseudomonas palustris strain PS3. PloS One 15 (7 July), 4–7.
Lozupone, C., et al., 2010. UniFrac: an effective distance metric for microbial community comparison'. ISME J. 5 (2), 169–172. Nature Publishing Group.
Lucia, D.S., et al., 2014. The Family Bradyrhizobiaceae. The Prokaryotes 135–154.
Luo, L., et al., 2019. The effects of Rhodopseudomonas palustris PSB06 and CGA009 with different agricultural applications on rice growth and rhizosphere bacterial communities. Amb. Express 9 (1). Springer Berlin Heidelberg.
Mainali, K.P., et al., 2017. Statistical analysis of co-occurrence patterns in microbial presence-absence datasets. PloS One 1–21.
Maryani, N., et al., 2019. Phylogeny and genetic diversity of the banana Fusarium wilt pathogen Fusarium oxysporum f. sp. cubense in the Indonesian centre of origin. Stud. Mycol. 92, 155–194. ELSEVIER B.V.
Mazurier, S., et al., 2009. Phenazine antibiotics produced by fluorescent pseudomonads contribute to natural soil suppressiveness to Fusarium wilt. ISME J. 3 (8), 977–991.
Mazzola, M., Freilich, S., 2017. Prospects for biological soil-borne disease control: application of indigenous versus synthetic microbiomes. Phytopathology 107 (3), 256–263.
Meghvansi, M.K., Varma, A., 2016. Organic amendments and soil suppressiveness in plant disease management. Choice Rev. Online.
Méndez-García, C., et al., 2018. Metagenomic Protocols and Strategies, Metagenomics: Perspectives, Methods, and Applications. Elsevier Inc.
Mohd Fishal, E.M., Meon, S., Yun, W.M., 2010. Induction of tolerance to fusarium wilt and defense-related mechanisms in the plantlets of susceptible berangan banana pre-inoculated with pseudomonas sp. (UPMP3) and burkholderia sp. (UPMB3)', *Agricultural Sciences in China*. Chin. Acad. Agricul. Sci. 9 (8), 1140–1149.
Moon-cheol, N., Song, L.W., Chan-sun, P., Min-soo, C., 2009. Novel Streptomyces argenteolus strain having activity aganist plant pathogens. Available at: https://patents.google.com/patent/KR101107331B1/en.
Mostert, D., et al., 2017. The distribution and host range of the banana Fusarium wilt fungus , Fusarium oxysporum f. sp. cubense, in Asia. PloS One 12 (7), 1–24.
Nikata, T., et al., 1996. Molecular analysis of the phosphate-specific transport (pst) operon of Pseudomonas aeruginosa. Mol. Gen. Genet. 250 (6), 692–698.
O'Neill, W.T., et al., 2016. Detection of Fusarium oxysporum f. sp. cubense tropical race 4 strain in northern Queensland', *Australasian Plant Disease Notes*. Australas. Plant Dis. Notes 11 (1), 10–12.
Oteino, N., et al., 2015. Plant growth promotion induced by phosphate solubilizing endophytic Pseudomonas isolates. Front. Microbiol. 6 (JUL), 1–9.
Parks, D.H., et al., 2014. STAMP: statistical analysis of taxonomic and functional profiles. Bioinformatics 30 (21), 3123–3124.
Patzer, S.I., Hantke, K., 1998. The ZnuABC high-affinity zinc uptake system and its regulator Zur in Escherichia coli. Mol. Microbiol. 28 (6), 1199–1210.
Quince, C., et al., 2017. Shotgun metagenomics , from sampling to analysis. Nat. Biotechnol. 35 (9), 833–844.
Ren, H., et al., 2020. Biochar and rhizobacteria amendments improve several soil properties and bacterial diversity. Microorganisms 8 (4), 1–17.
Rodríguez, H., Fraga, R., 1999. Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol. Adv. 17 (4–5), 319–339.
Rodriguez, M.A.D., Vicente, L.P., Martínez, E., 2014. Technical Manual Prevention and diagnostic of Fusarium Wilt (Panama disease) of banana caused by Fusarium oxysporum f.sp. cubense Tropical Race 4 (TR4)'. Workshop Diag. Fusarium Wilt 4 (May), 1–74.
Rojas-rojas, F.U., et al., 2018. Broad-spectrum antimicrobial activity by Burkholderia cenocepacia TAtl-371 , a strain isolated from the tomato rhizosphere. Microbiology 164, 1072–1086.
Ruanpanun, P., et al., 2010. Actinomycetes and fungi isolated from plant-parasitic nematode infested soils: screening of the effective biocontrol potential, indole-3-acetic acid and siderophore production. World J. Microbiol. Biotechnol. 26 (9), 1569–1578.
Saharan, B., Nehra, V., 2011. Plant growth promoting rhizobacteria: a critical review. Life Sci. Med. Res. 21, 1–30.
Sait, M., Davis, K.E.R., Janssen, P.H., 2006. Effect of pH on isolation and distribution of members of subdivision 1 of the phylum Acidobacteria occurring in soil. Appl. Environ. Microbiol. 72 (3), 1852–1857.
Schlatter, D., et al., 2017. Disease suppressive soils: new insights from the soil microbiome. Phytopathology 107 (11), 1284–1297.
Schreiber, K.H., O'Leary, M.N., Kennedy, B.K., 2016. The mTOR pathway and aging. In: Handbook of the Biology of Aging, eighth ed., pp. 55–81.
Shen, Z., et al., 2015. Soils naturally suppressive to banana Fusarium wilt disease harbor unique bacterial communities. Plant Soil 393 (1–2), 21–33.
Simonetti, E., et al., 2018. A novel Burkholderia ambifaria strain able to degrade the mycotoxin fusaric acid and to inhibit Fusarium spp . growth. Microbiol. Res. 206 (September 2017), 50–59. Elsevier.
Smanski, M.J., et al., 2009. Engineered Streptomyces platensis strains that overproduce antibiotics platensimycin and platencin. Antimicrob. Agents Chemother. 53 (4), 1299–1304.
Staunton, J., Wilkinson, B., 1999. Biosynthesis of erythromycin and related macrolides. In: Barton, S.D., Nakanishi, K., Meth-Cohn, O., B. T.-C. N. P. C. (Eds.), Comprehensive Natural Products Chemistry. Pergamon, Oxford, pp. 495–532.
Su, H., Hwang, S., Ko, W., 1986. Fusarial wilt of cavendish bananaas in Taiwan. Plant Dis. 70 (9).
Su, P., et al., 2017. Photosynthetic bacterium Rhodopseudomonas palustris GJ-22 induces systemic resistance against viruses. Microbial. Biotechnol. 10 (3), 612–624.
Suweis, S., et al., 2013. Emergence of structural and dynamical properties of ecological mutualistic networks. Nature 500, 3–6. Nature Publishing Group.
Sy, A., et al., 2001. Methylotrophic Methylobacterium bacteria nodulate and fix nitrogen in symbiosis with legumes. J. Bacteriol. 183 (1), 214–220.
Tabassum, B., et al., 2017. Bottlenecks in commercialisation and future prospects of PGPR. Appl. Soil Ecol. 121 (October), 102–117. Elsevier.
Thangavelu, R., et al., 2003. The effect of Pseudomonas fluorescens and Fusarium oxysporum f.sp. cubense on induction of defense enzymes and phenolics in banana. Biol. Plant. (Prague) 46 (1).
Tian, B., Yang, J., Zhang, K.Q., 2007. Bacteria used in the biological control of plant-parasitic nematodes: populations, mechanisms of action, and future prospects. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 61 (2), 197–213.
Van Bruggen, A.H.C., Semenov, A.M., 2000. In search of biological indicators for soil health and disease suppression. Appl. Soil Ecol. 15, 13–24.
Vessey, J.K., 2003. Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255 (2), 571–586.
Voora, V., Larrea, C., B, S., 2020. Global market report: bananas. Exchange Organ. Behav. Teach J. 62. Available at: https://www.iisd.org/system/files/publications/ssi-global-market-report-banana.pdf.
Wang, Q., et al., 2018. Efficient culture of Rhodopseudomonas palustris using landfill leachate. J. Pure Appl. Microbiol. 12 (4), 1679–1687.
Ward, N.L., et al., 2009. Three genomes from the phylum Acidobacteria provide insight into the lifestyles of these microorganisms in soils†. Appl. Environ. Microbiol. 75 (7), 2046–2056.
Weller, D.M., et al., 2002. Microbial populations responsible for spesific soil suppressiveness to plant pathogens. Annu. Rev. Phytopathol. 40 (1), 309–348.
Widder, S., et al., 2014. Fluvial network organization imprints on microbial co-occurrence networks. Proc. Natl. Acad. Sci. Unit. States Am. 111 (35), 12799–12804.
Wolińska, A., 2019. Metagenomic Achievements in Microbial Diversity Determination in Croplands. Microb. Divers. Genom. Era 1992, 15–35.
Wong, W.-T., et al., 2014. Promoting effects of a single Rhodopseudomonas palustris inoculant on plant growth by Brassica rapa chinensis under low fertilizer input. Microb. Environ. 29 (3), 303–313.
Xu, Z., et al., 2020. Isolation of burkholderia sp. HQB-1, A promising biocontrol bacteria to protect banana against Fusarium wilt through phenazine-1-carboxylic acid secretion. Front. Microbiol. 11 (December), 1–12.
Yabe, S., et al., 2017. Dictyobacter aurantiacus gen. nov., sp. nov., a member of the family Ktedonobacteraceae, isolated from soil, and emended description of the genus thermosporothrix. Int. J. Syst. Evol. Microbiol. 67 (8), 2615–2621.
Yi, Y., et al., 2017. Comparative transcriptomics of Bacillus mycoides strains in response to potato-root exudates reveals different genetic adaptation of endophytic and soil isolates. Front. Microbiol. 8 (August), 1–14.
Yu, X., et al., 2011. The siderophore-producing bacterium, Bacillus subtilis CAS15, has a biocontrol effect on Fusarium wilt and promotes the growth of pepper. Eur. J. Soil Biol. 47 (2), 138–145. Elsevier Masson SAS.