BIODIVERSITAS
Volume 25, Number 7, July 2024
Pages: 2828-2838

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d250704

Diversity of endophytic bacteria in two banana cultivars and their potential for plant growth promoter

TRIASTUTI RAHAYU[1,2,♥], YEKTI ASIH PURWESTRI[3,6], SITI SUBANDIYAH[3,4], YASIR SIDIQ[2], DONNY WIDIANTO[1,5,♥♥]

[1]Graduate School of Biotechnology, Universitas Gadjah Mada. Jl. Teknika Utara, Sleman 55284, Yogyakarta, Indonesia. Tel.: +62-274-564305, Fax.: +62-274-520842, ♥email: tr124@ums.ac.id
[2]Department of Biology Education, Universitas Muhammadiyah Surakarta. Jl. A. Yani, Sukoharjo 57162, Central Java, Indonesia
[3]Research Center for Biotechnology, Universitas Gadjah Mada. Jl. Teknika Utara, Sleman 55281, Yogyakarta, Indonesia
[4]Department of Plant Protection, Faculty of Agriculture, Universitas Gadjah Mada. Jl. Flora, Bulaksumur, Sleman 55281, Yogyakarta, Indonesia. Tel.: +62-274-563062, ♥♥email: donny@ugm.ac.id
[5]Department of Agricultural Microbiology, Faculty of Agriculture, Universitas Gadjah Mada. Jl. Flora, Bulaksumur, Sleman 55281, Yogyakarta, Indonesia
[6]Faculty of Biology Universitas Gadjah Mada. Jl. Teknika Selatan, Sekip Utara Bulaksumur Sleman 55281, Yogyakarta, Indonesia

Manuscript received: 15 January 2024. Revision accepted: 3 July 2024.

Abstract. *Rahayu T, Purwestri YA, Subandiyah S, Sidiq Y, Widianto D. 2024. Diversity of endophytic bacteria in two banana cultivars and their potential for plant growth promoter. Biodiversitas 25: 2828-2838.* The Klutuk banana plant (*Musa balbisiana* colla) is recognized as a resistant plant against biotic and abiotic stresses. The resistance trait of the cultivar is not exactly revealed but is most likely related to the presence of endophytic bacteria. This study aimed to determine the variation of banana cultivars and their organs on endophytic bacterial populations and their character as plant growth promoters (PGP). The study involved isolating endophytic bacteria from the root, corm, and petiole of cv. Klutuk and cv. Ambon, aged 4-5 months. Isolated endophytic bacteria were evaluated based on plant-growth-promoting (PGP) criteria. Subsequently, 16S rRNA sequences were amplified using 16S primers, 27f and 1492r, then sequenced. The obtained isolates were also identified by comparing the 16S sequences to the NCBI gene bank. The results showed that the population and number of isolates with the most PGP characters were in both banana cultivars' roots, petiole, and corm. Endophytic bacteria with multiple traits as PGP are composed of Phylum Proteobacteria (gamma, alpha, beta), Firmicutes, and Actinobacteria members. Several species are potential as they have multiple PGP traits with high-quantity test results, namely *Microbacterium testaceum* DSM 20166 strain, *Simplicispira* sp. CPCC 100842 strain, *Klebsiella grimontii* SB73 strain, *Enterobacter mori* LMG 25706 strain, *Pantoea* sp. CoA11 strain, *Agrobacterium tumefaciens IAM 12048*, *Variovorax guangxiensis* GXGD002 strain, *Serratia nematodiphila* DZ0503SBS1 strain, *Bosea thiooxidans* BI-42 strain, *Erwinia tasmaniensis* Et1/99 strain, *Methylobacterium fujisawaense* DSM 5686 strain, K2 isolate, K8 isolate, and K18 isolates. This study also revealed the endophytic bacterial population and character as plant organs influenced PGP. The roots and petioles became the banana plant organs colonized by endophytic bacteria with multiple traits as PGP. Overall, several isolates were discovered in cv. Klutuk were suspected of being new species with potential as PGP agents, and these were not identified in cv. Ambon.

Keywords: Ambon banana, endophytic bacteria, klutuk banana, plant growth promoter, plant organs

INTRODUCTION

Musa balbisiana colla cv. Klutuk is a BB genome cultivar and is known as a resistant cultivar against biotic stresses such as *Xanthomonas* (Tripathi et al. 2019), Fusarium wilt (Maryani et al. 2019), and herbivore (Hölscher et al. 2016). In addition, this cultivar is resistant to drought stress (Ravi et al. 2013; Kallow et al. 2020). The resistance of Klutuk banana causes this cultivar to have a wide distribution in Indonesia (Sunandar 2017). Whereas *Musa acuminata* cv. Ambon with AAA genome is more susceptible than Klutuk banana (Kissel et al. 2015; Vanhove et al. 2012; Tripathi and Odipio 2008; Maryani et al. 2019). Previous studies showed that these two cultivars have different consortiums of endophytic bacteria (Rahayu et al. 2021). The difference was related to the resistance of Klutuk and the susceptibility of Ambon banana (Rahayu et al. 2021). In addition, the roles of endophytic bacteria have been reported as plant protectors against rice leaf blight pathogen (Djatmiko et al. 2023), fungal plant pathogen *Colletotrichum scovillei* (Wei et al. 2023), anthracnose disease in chili plant (Nurbailis et al. 2023), and Botrytis cinerea fungal pathogen (Hamane et al. 2023).

Besides improving plant resistance, endophytic bacteria increase plant growth and productivity. Plant growth and yield enhancements by endophytic bacteria have been shown by several reports (Forte et al. 2023; Aini et al. 2023; Lovecká et al. 2023; Zhao et al. 2023). Consortium and single inoculation of rice root using endophytic bacteria from Klutuk banana plants improves the growth and yield both at 30 and 140 days after plantation (Rahayu et al. 2023). Application of endophytic bacteria strain *Serratia marcescens* with potassium addition increased the root weight of paddy in an acidic soil environment (Sutio et al. 2023).

Endophytic bacteria in the plant tissue respond faster if the host plant is subjected to biotic or abiotic stress. This role is related to its character as a plant growth promoter

(PGP): N fixation, producing indole acetic acid (IAA) and siderophore, having ACC deaminase activity, dissolving PO_4, and inhibiting phytopathogens (de Fretes et al. 2018; Miliute et al. 2015; Santoyo et al. 2016). Commonly, a resistant plant against biotic and abiotic stresses involves the role of endophytic bacteria. Therefore, endophytic bacteria is a useful biofertilizer property that supports sustainable agriculture. A bibliometric analysis summarized that biofertilizer improves plant growth through plant hormone regulation, optimization of plant nutrition, soil environment, and microbiome improvements (Zhao et al. 2024).

Recently, there have been many isolations and characterizations of endophytic bacteria as PGP from banana plants, especially from roots and leaves (Karthik et al. 2017; Marcano et al. 2016; Souza et al. 2013), while isolation from the corm and petiole is still rarely conducted. Corm is an essential banana plant organ because it is the only organ for vegetative reproduction. Information about the colonization of endophytic bacteria in corms is still very limited; therefore, this study used root, corm, and petiole as the banana plant organs. Root and corm represent the underground compartment, while petioles represent the aboveground compartment. Meanwhile, it was reported that parts of the plant are colonized by different bacterial groups (Coleman-Derr et al. 2015).

It is crucial to characterize the bacteriome of those two banana cultivars; furthermore, this study explored the difference in the bacteria inside the two banana cultivars. Specifically, this study characterized bacteria inside each cultivar's three organs and explored their potential as plant growth promoters. Therefore, this study aimed to determine the effect of plant organs and banana cultivars on endophytic bacterial populations and their characteristics as PGP. It is expected to obtain comprehensive information about the relationship between banana plant organs and endophytic bacterial populations, species, and their characteristics as PGP. Furthermore, the obtained data could be beneficial to designing targeted bio-fertilizers to promote banana plant growth and biocontrol.

MATERIALS AND METHODS

Sampling and surface sterilization

Two banana cultivars (cv. Klutuk BB and cv. Ambon AAA) were collected from loamy sandy (LS) and silt loam (SL) soils with the location coordinates and the physio-chemical properties of the soil attached to Table 1. Three ready-planting suckers aged 4-5 months were selected for each cultivar on each soil type to ensure the consistency of bacteriomes in different soils. Then the endophytic bacteria were isolated from root, corm, and petiole. All samples were stored in sterile propylene bags and a coolbox at 4°C. Next, plant organs were washed in running water and sterilized using 70% ethanol for 2 minutes. After that, it was soaked in 1.5% sodium hypochlorite for 10 minutes with occasional shake. Then, the sample was rinsed using sterile distilled water 5 times and drained with thick tissue. To confirm the effectiveness of the surface sterilization of the material, the last sterile distilled water to rinse was plated on the TSA media using the spread plate method and incubated for 48 hours at room temperature; those treatments to ensure there should be no bacterial or fungal grown. Hence, if there is still contamination, the material sterilization is repeated (Karthik et al. 2017; Sekhar and Thomas 2015).

Bacterial isolation

Therefore, 1 g of sterile plant tissue was mashed using a sterile mortal while adding 4 mL of peptone salt. Furthermore, two dilutions of 10^{-1} and 10^{-3} uses peptone salt. Next, 100 µL of each 10^{-1} and 10^{-3} dilutions were inoculated (plating) on tryptic soy agar (TSA) and NA media using the spread plate method. Incubation was carried out at room temperature for 72 hours (Karthik et al. 2017), and after that, the endophytic bacterial population/gram fresh weight of tissue was calculated. Single colonies at the highest dilution and morphologically different were subcultured to other TSA media to obtain pure culture. Slant cultures were incubated for 48 hours at room temperature and then refrigerated for variability analysis using rep PCR.

Rep-PCR analysis of endophytic bacteria

Each isolate was grown in 5 mL of TSB medium for 24 hours at 37°C with a 180-rpm shaker. Cells were harvested by centrifugation at 13,000 rpm for 10 minutes; then, the bacterial DNA genome was isolated using Presto™ Mini gDNA Bacteria Kit. The PCR rep used the BOXA1R (5'-CTCCGGCAAGGCGACGCTGAC-3') primer. Rep PCR products were visualized using 12% polyacrylamide gel electrophoresis (PAGE) with silver nitrate staining and a 100-bp DNA ladder marker. Next, the Simple Matching Coefficient was used to determine the similarity value among bacterial strains. Clustering analysis was performed using the UPGMA (Unweight Pair Group Method with Averages) algorithm to present the analysis results as a dendrogram to determine the diversity and similarity between isolates (Souza et al. 2013).

Table 1. Sampling location and results of soil physics analysis

Soil type	Sampling point coordinates	Sand (%)	Dust (%)	Clay (%)	pH	C org (%)	N Tot (%)	C/N	K (ppm)	P_2O_5 (ppm)
Loamy Sandy (LS)	110°20'14″-110°21'48″	77.8	19.75	2.5	6.79	1.98	0.083	45	58	23.75
Silt Loam (SL)	110°12′1″-110°12′57″	43.8	42.75	12	7.18	1.59	0.03	53	71	53.5

Characterization of endophytic bacteria isolates as PGP

Nitrogen fixation was tested using nitrogen-free broth (NFb). Bacterial isolates were grown in culture tubes containing 7 mL of NFb medium. Next, 5 µL of bacterial suspension (OD=1.0 ABS, λ=540 nm) was transferred to a tube containing 7 mL of semisolid NFb medium. The test tube was incubated at 28°C for 7 days. After incubation, pellicle formation is a free-living diazotroph (Andrade et al. 2014).

IAA production was tested using the colorimetric method (Wang et al. 2016). Endophytic bacterial isolates were inoculated in a test tube containing 5 mL of TSB medium containing 1 mg/mL L-tryptophan at pH 7.0 and incubated at room temperature for 24-48 hours with shaking. The supernatant was separated from the cell by centrifugation at 13,000 rpm for 10 minutes. Finally, 1 mL of the supernatant was mixed with 2 mL of Salkowski's reagent (50 mL 35% $HClO_4$ and 1 mL 0.5 M $FeCl_3.6H_2O$) and left for ± 30 minutes to form a pink color. The IAA concentration was analyzed using a spectrophotometer at λ 530 nm based on a standard curve.

ACC-deaminase activity was tested by inoculating endophytic bacterial isolates on DF (Dworkin and Foster) media as a negative control, DF+ammonium sulfate as a positive control, and DF+AIB 3 mM as a testing medium. Petri was incubated at room temperature for 72 hours. The growth of isolates in the DF+AIB medium was compared with positive and negative controls; the growth in DF+AIB media showed the ability of isolates to use AIB as a nitrogen source (Ali et al. 2014).

Siderophore production was measured using the modified microplate method (Arora and Verma 2017). Then, 100 µL of supernatant from the liquid culture of endophytic bacteria with a cell density of 10^8 cfu/mL was put in separate microplate wells and added with 100 µL of CAS reagent. After incubation, the optical density of each sample (placed in microplate wells) was recorded at 630 nm using a microplate reader (Spectra Max M5e). The siderophore produced by strains was measured in percent siderophore unit (psu), which was calculated according to the following formula:

Siderophore production (psu) = (Ar-As) x 100/Ar

Where:

Ar : absorbance of reference (chrome azurol S (CAS) solution and uninoculated broth)

As : absorbance of the sample (CAS solution and cell-free supernatant of sample)

Phosphate solubilization was tested on Pikovskaya (PVK) medium containing 10 g glucose; 5 g Ca3(PO4)2; 0.5 g (NH4)2SO4; 0.2 g NaCl; 0.1 g MgSO4·7H2O; 0.2 g KCl; 0.5 g yeast extract; 0.002 g MnSO4·H2O; and 0.002 g FeSO4·7H2O in 1 L of media. The well was made in the middle of the petri using a sterile cork borer with a diameter of 6 mm and then filled with 10 µL of endophytic bacterial suspension cultured in 24-hour TSB media. Furthermore, petri was incubated in an incubator at 28°C for 15 days. The solubilization zone and bacterial colony diameter were measured to calculate the solubilization index (SI) using the formula:

Phosphate Solubilization Index (SI) = (colony diameter + halo zone diameter)/colony diameter

Solubilization efficiency is assessed on a scale in which values <1.0 are classified as very low, 1.0-2.0 are classified as low, 2.0-3.0 are classified as medium, and >3.0 are classified as high (Matos et al. 2017).

The antifungal activity was performed using a dual culture inhibition assay on PDA media. Agar plug fungi (fungal plug) 10 mm diameter *Fusarium oxysporum* f. sp. *cubense* of 5 days old was placed in the middle of the petri and then incubated for 3 days. After incubation, endophytic bacteria isolates for 2 days on TSA media were streaked at 2 cm from the tested fungi. Petri was incubated at 28°C for 7 days, and the percent inhibition was measured using the formula:

Inhibition (%) = [(R - r)/R × 100]

Where: r is the radius of the fungal colony opposite the bacterial colony; R is the maximum radius of the fungal colony away from the bacterial colony.

Identification of endophytic bacterial isolates

Potential endophytic bacterial isolates were identified based on the 16S rRNA gene amplified using universal primers 27f (5′- AGAGTTTGATCCTGGCTCAG-3′) and 1492r (5′- GGTTACCTTGTTACGACTT-3′). Sequencing analysis using reverse and forward primers on the Hitachi AB biosystem machine, GA3500. The two-way sequencing results were sampled using DNA baser assembler software, and then the 16S rRNA base sequences were compared using BLAST on the NCBI website. The 16S rRNA gene sequence is stored in GenBank with an accession number, as shown in Table 2.

Table 2. Isolates ID and GenBank accession number

No.	Isolate ID	GenBank accession no.
1	r_K1	MW077302
2	r_K2	Low similarity
3	r_K3	MW079852
4	r_K7	MW079851
5	r_K8	Low similarity
6	r_K10	MW079893
7	r_K14	MW079895
8	p_K18	Low similarity
9	p_K22	MW080646
10	p_K25	MW080364
11	r_K35	MW079897
12	p_K58a	MW080538
13	r_K75	MW079920
14	r_K86	MW131458
15	r_K111	MW079900
16	r_K114	MW079902
17	r_K115	chimeric
18	r_K117	MW079906
19	r_K324	MW079909
20	p_A9	chimeric
21	r_A22	MW133040
22	r_A24	MW133042
23	p_A30	MW126635
24	c_A31	chimeric
25	c_A34	PQ113680
26	r_A41	MW133043
27	r_A44b	MW130087
28	r_A50	MW133727
29	r_A51	MW131504

Statistical analysis

Endophytic bacterial population data were analyzed using one-way analysis of variance (ANOVA) with SPSS software package for Windows (SPSS, version 10.0). If statistical significance (P=0.05) was significant, the mean values were further separated using Duncan's multiple range test (DMRT). Principal component analysis (PCA) for endophytic bacterial populations and their characteristics as PGP were analyzed using Minitab19 software.

RESULTS AND DISCUSSION

Endophytic bacterial population and analysis of variability using rep PCR

The study revealed the sequence of the largest population of endophytic bacteria was in the roots ($5.9x10^2$-$2.3x10^4$ CFU/g tissue), followed by the petiole ($0.5x10^1$-$1.9x10^3$ CFU/g tissue) and the last one was corm ($0.1x10^1$-$1.9x10^1$ CFU/g tissue) of the two banana cultivars grown on LS and SL soil. Different plant organs show significant differences in endophytic bacterial populations. Meanwhile, TSA and NA media use when isolating endophytic bacteria was not significantly different (Table 3).

Plant parts appear to influence the endophytic bacterial population and the number of isolates with PGP characteristics compared to banana cultivars and soil types (Table 3; Figures 2.A and 2.B). Roots are directly related to soil, in which rhizosphere soil contains 10^8-10^9 CFU/g bacteria. In contrast, the phylosphere and endosphere have a small population of microbes, namely around 10^2-10^4 CFU/g samples (Sekhar and Thomas 2015; Thomas and Soly 2009). The presence of root exudate is an attractant for bacteria to approach and enter the roots (Santoyo et al. 2016) through root hairs as the main entry point, then colonization occurs in the root cortex and vascular tissue (Prieto et al. 2011; Souza et al. 2016). Corms are organs close to roots and in the soil but have the least endophytic bacterial population (Table 3). These results are consistent with the research of Thangavelu and Gopi (2015), who have analyzed the endophytic bacteria from banana plants to suppress Fusarium wilt disease.

Table 3. Mean CFU of Klutuk and Ambon Cultivars Grown into LS and SL Soil. Different uppercase letters showed significant differences according to Duncan's multiple range test ($p< 0.05$). CFU value is the mean of four replications

Soil types	Cultivars	Organ	Samples code	Mean CFU/g tissue*	
				TSA medium	NA medium
LS	Klutuk	Root	RKL	$1.1 \times 10^3 \pm 1.70^{c}$	$4.9 \times 10^2 \pm 1.26^{d}$
		Corm	CKL	$0.5 \times 10^1 \pm 1.50^{a}$	$1.9 \times 10^1 \pm 2.08^{abc}$
		Petiole	PKL	$1.8 \times 10^1 \pm 0.84^{ab}$	$1.8 \times 10^1 \pm 1.04^{abc}$
	Ambon	Root	RAL	$1.5 \times 10^3 \pm 1.58^{c}$	$7.7 \times 10^2 \pm 2.78^{cd}$
		Corm	CAL	$0.1 \times 10^1 \pm 0.80^{a}$	$0.1 \times 10^1 \pm 0.80^{a}$
		Petiole	PAL	$2.5 \times 10^1 \pm 1.76^{ab}$	$5.5 \times 10^1 \pm 2.23^{abc}$
SL	Klutuk	Root	RKS	$2.3 \times 10^4 \pm 1.28^{d}$	$2.1 \times 10^4 \pm 1.68^{e}$
		Corm	CKS	$0.5 \times 10^1 \pm 1.32^{a}$	$1.3 \times 10^1 \pm 1.85^{abc}$
		Petiole	PKS	$1.9 \times 10^3 \pm 3.24^{bc}$	$1.6 \times 10^3 \pm 3.65^{bcd}$
	Ambon	Root	RAS	$5.9 \times 10^2 \pm 0.78^{c}$	$7.0 \times 10^2 \pm 1.17^{de}$
		Corm	CAS	$1.4 \times 10^1 \pm 1.85^{a}$	$1.5 \times 10^1 \pm 1.91^{abc}$
		Petiole	PAS	$1.8 \times 10^1 \pm 1.99^{ab}$	$0.5 \times 10^1 \pm 1.33^{abc}$

Table 4. The number and percentage of endophytic bacterial isolates isolated from the root, petiole, and corm of the banana plant cv. Klutuk and cv. Ambon, grown on LS and SL lands, can become a PGP

Soil types	Cultivars	Part of plant	Number of isolates	Number and percentage of isolates that have PGP characters											
				A	%	B	%	C	%	D	%	E	%	F	%
LS	Klutuk	Root	25	19	76	14	56	6	24	16	64	9	36	8	22.2
		Petiole	20	15	75	6	30	1	5	6	30	4	20	3	15
		Corm	6	5	83.3	0	0	0	0	4	66.7	0	0	2	33.3
	Ambon	Root	12	8	66.7	4	33.3	5	41.7	10	83.3	1	8.33	2	16.7
		Petiole	5	3	60	1	20	2	40	1	20	3	60	0	0
		Corm	1	0	0	0	0	0	0	1	100	0	0	0	0
SL	Klutuk	Root	24	20	83.3	5	20.8	4	16.7	9	37.5	8	33.3	5	20.8
		Petiole	12	5	41.7	4	33.3	0	0	9	75	2	16.7	2	16.7
		Corm	1	0	0	0	0	0	0	1	100	0	0	0	0
	Ambon	Root	11	10	90.9	6	54.5	2	18.2	1	9.09	4	36.4	3	27.3
		Petiole	2	2	100	1	50	1	50	1	50	1	50	1	50
		Corm	9	7	77.8	2	22.2	3	33.3	4	44.4	2	22.2	1	11.1
Total			128	94		43		24		63		34		27	
Average (%)					62.9		26.7		19.1		56.7		23.6		17.8

Note: A: N fixation (+, ++, or -), B: IAA production (ppm), C: ACC deaminase activity (+ or -), D: siderophore production >25%, E: PO_4 solubilization (index), F: antifungal activity against to Foc (%)

A total of 169 isolates were successfully made into pure culture. Furthermore, diversity analysis was carried out using rep PCR. The results of the PCR rep analysis showed that 159 isolates had different band patterns, indicating different strains (Figure 1). Ten isolates with similar band patterns indicated the same strain of endophytic bacteria. The varied amplicon of 159 isolates was analyzed, and a dendrogram was developed to determine the genetic diversity and similarity among isolates (Figure 1).

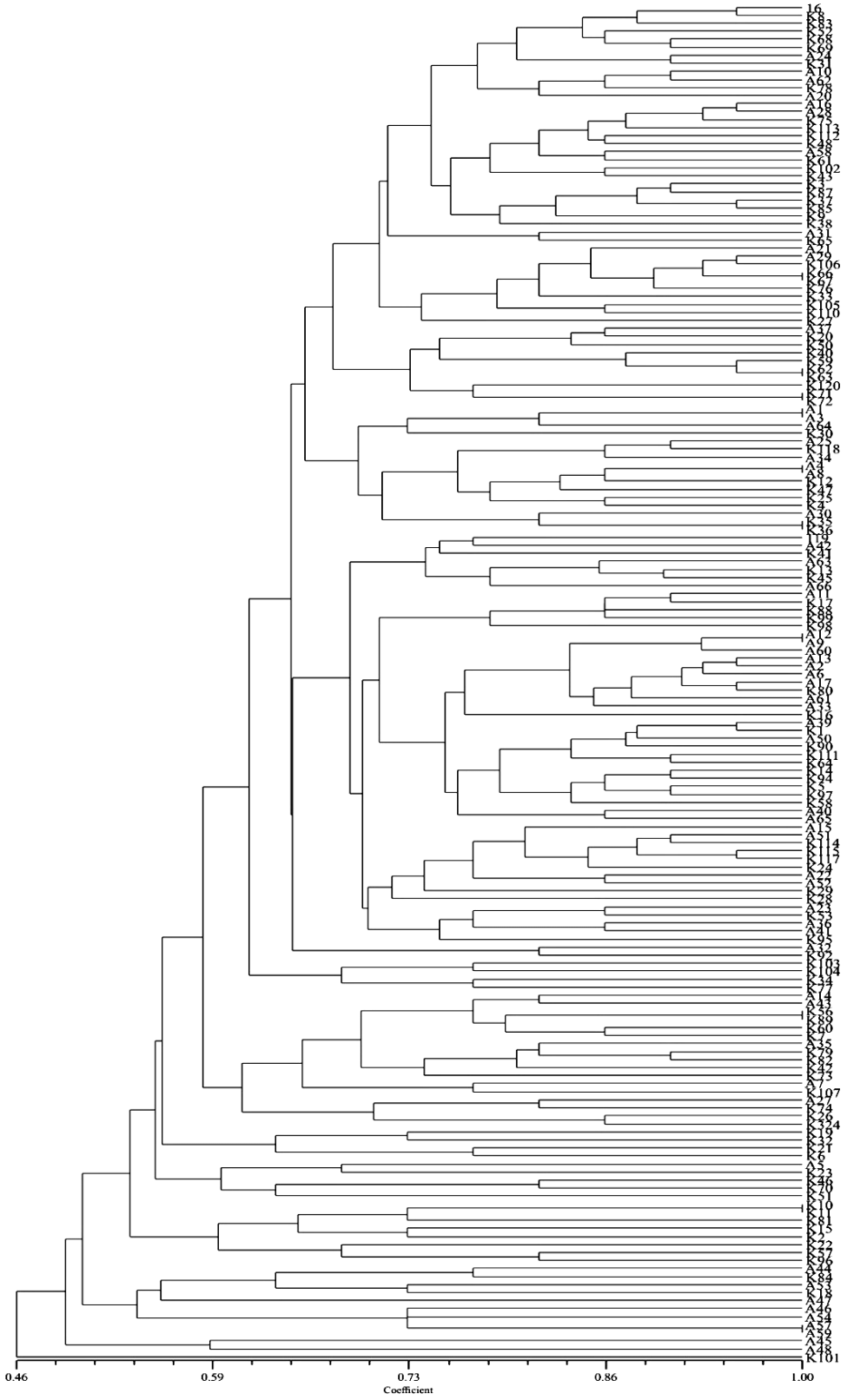

Figure 1. Dendrogram of all isolated endophytic bacteria

Table 5. Bacterial population (CFU) in banana leaf axillary

Samples	CFU/mL
P1	1.67×10^5
P2	2.15×10^6
P3	1.89×10^5
P4	2.33×10^5
Average	6.32×10^5

Plant anatomical structures can inhibit the colonization of endophytic bacteria into plants as a physical barrier (Galindo-Castañeda et al. 2019; Kumar et al. 2020). Corm consists of 2 zones, namely peripheral and central. The peripheral zone comprises a network of small parenchyma cells with small transport bundles. The central zone comprises parenchyma cells larger than the peripheral zone (Sumardi and Wulandari 2010). In this study, we used the central corm. The anatomical structure of the corm appears to be an obstacle to the colonization of endophytic bacteria or other biochemical barriers. Microbiome data and colonization of endophytic bacteria on banana corms are essential, considering that the corm is the only vegetative reproductive organ for banana plants (Robinson and Saúco 2010) and is the second organ after roots colonized by hyphae *Fusarium oxysporum* f.sp. *cubense* (Foc) (Li et al. 2017; Warman and Aitken 2018). This fungus is the most destructive disease of this crop (Ploetz 2015). Therefore, it is still necessary to do an in-depth study of the microbiota colonization in banana corms. Furthermore, this data can be used to formulate the right strategy for overcoming problems related to banana plant growth.

Petioles located far from the roots have a higher population than corms. This may be related to the petiole's anatomical structure, which has stomata in which the stomata are one of the entry points for endophytic bacteria and are composed of very large parenchyma tissue (Liu et al. 2017). The hollow U-shaped petioles allow the storage of microbes so that the bacterial population in the banana leaf axillary is relatively high (6.32 CFU/mL) (Table 5). Furthermore, if there is a wound on the tissue, the bacteria will enter and colonize it.

Characterization of endophytic bacteria isolates as PGP

N fixation is most often possessed by endophytic bacterial isolates with the highest mean percentage (94 isolates, 62.9%). Siderophore production >25% (63 isolates, 56.7%), IAA production (43 isolates, 26.7%), PO_4 solubilization (34 isolates, 23.6%), antifungal activity against Foc (27 isolates, 17.8%), and the least was ACC deaminase activity (24 isolates, 19.1%). Endophytic bacteria isolated from cv. Klutuk has more complete including the percentage of each PGP than cv. Ambon on both LS and SL lands. It can be inferred from Table 4 that endophytic bacterial isolates from the Klutuk cultivar have a higher percentage in most PGP characters than Ambon cultivar.

The number of isolated bacteria in this study, 128 isolates, was relatively high compared to other studies that isolated bacteria from several banana plant organs. A study of endophytic bacterial isolation from root, rhizome, pseudostem, petiole, and leaves of healthy banana plants reported 38 total isolates. Among them, 16 strains exhibited inhibition against rot disease factor, *Pectobaterium carotovorum* (Ragavi et al. 2019). Kara and Soylu (2021) isolated 23 endophytic bacteria from banana plants' fruits, stems, and leaves with one species, *Bacillus mojavensis*, promising biocontrol against *Fusarium verticillioides*.

In addition, the number of isolates showing PGP characters ranged from 24 (ACC deamination) to 94 (N fixation) isolates was also high. A study reported endophytic bacterial isolation from five different banana cultivars resulted in 352 bacterial isolates, with only 17 isolates showing indole acetic acid synthesis and siderophore production (Karthik et al. 2017). Also, Vaidya et al. (2021) stated that 2 isolates out of 21 isolated bacteria from banana plants showed PGP activities.

The characterization results as PGP obtained 29 isolates with multiple traits of potential PGP with roots and petiole of cv. Klutuk with 15 and 4 strains); meanwhile, isolates from roots, petiole, and corm cv. Ambon are 6, 2, and 2 strains, respectively (Table 6). These isolates have been identified based on 16S rRNA with % identity between 90.47-100% except for K2, K8, and K18, with % identity of 79.75, 80.54, and 79.50%, respectively.

The highest IAA production was produced by the K2 strain, as much as 73.5 ppm, followed by *Pseudescherichia vulneris* strain NBRC 102420, *Variovorax guangxiensis* strain GXGD002, *Brachybacterium huguangmaarense* strain M1, *Enterobacter mori* LMG, and *Pantoea dispersa* strain: DSM 30073. The PGPB tested were *Microbacterium testaceum* strains DSM 20166 and *Simplicispira* sp. CPCC 100842; meanwhile, those that had 5 PGP characters tested were strains K2, K8, *Klebsiella grimontii* strain SB73, and *Enterobacter mori* LMG 25706. Species *Klebsiella grimontii* strain SB73, *Pantoea* sp. strain CoA11, *Agrobacterium tumefaciens* strain IAM 12048, *Variovorax guangxiensis* strain GXGD002, *Serratia nematodiphila* DZ0503SBS1, *Bosea thiooxidans* strain BI-42, *Erwinia tasmaniensis* Et1/99, and Methylobacterium fujisawaense strain DSM 5686 which were tested had 4 characters. For species potentially inhibiting *Fusarium oxysporum* f. sp. *cubense* is a strain of K18, *Pantoea* sp. strain CoA11, *Erwinia tasmaniensis* Et1/99, *Enterobacter mori* LMG 25706, *Serratia nematodiphila* DZ0503SBS1, *Agrobacterium tumefaciens* strain IAM 12048, *Variovorax guangxiensis* strain GXGD002, *Microbacterium testaceum* strain DSM 20166, and *Klebsiella grimontii* strain SB73 (Table 6).

The characteristics of endophytic bacterial isolates as PGP varied among samples. Endophytic bacteria with multiple traits as PGP are composed of members of Phylum Proteobacteria (Gamma, Alpha, Beta), Firmicutes, and Actinobacteria. The three phyla are reported to have many characteristics as PGPB from banana plants (Karthik et al. 2017; Kaushal et al. 2020; Liu et al. 2017; Sekhar and Thomas 2015). In this study, Gammaproteobacteria classes with three ordos and a total of 62 species dominated the banana bacteriome on cv. Klutuk and has characters as PGP (Table 8). These Gammaproteobacteria are reported to play a role in plant fitness and health (Karthik et al. 2017; Köberl et al. 2018; 2017). Gammaproteobacteria classes

dominate due to the presence of the order Pseudomonadales, which is widely known as PGP. Acinetobacter and Pseudomonas, as members of the Pseudomonadales order, are reported to be able to produce IAA, phosphate solubilization, ACC deaminase activity, siderophore and hydrogen cyanide production (Ali et al. 2014; Meliani et al. 2017; Patel et al. 2017; Paul and Sinha 2017; Pinski et al. 2019; Sachdev et al. 2010; Samaddar et al. 2019; Santoyo et al. 2012). The colonization of *Acinetobacter* and *Pseudomona*s, with respectively 38 and 30 genera members showing PGP characters (Table 2), was also evenly distributed in almost all parts of the plant (Pseudomonadales ordo in Table 8). It might be because they have secretion systems of types I, II, III, IV, V, and VI, which are related to the ability to colonize into the host, produce a polysaccharide capsule, tolerant to hydrogen peroxide, biofilm-producing organisms (Pinski et al. 2019; Harding et al. 2018; Bigot and Salcedo 2017; Repizo 2017). Secretion type I-VI is also commonly related to virulent protein transportation outside the cell (Green and Mecsas 2016). Specifically, most of Acinetobacter genus use type VI secretion, which releases effector proteins to colonize the host cells (Hernandez et al. 2020; Lewis et al. 2020). In the same way, Pseudomonas utilizes type III secretion (Horna and Ruiz 2021) to enter the host cells. *Pseudomonas* is also a producer of siderophore, which has a high affinity for iron, synthesizes antibiotics, and induces systemic resistance in plants (Santoyo et al. 2012).

Moreover, 29 strains are potential because they have multiple PGP traits with a high quantity of test results. These species are *Klebsiella grimontii, Acinetobacter oryzae, Pantoea* sp., *Pseudescherichia vulneris, Bacillus kochii, Brachybacterium huguangmaarense, Enterobacter cloacae* subsp. dissolvens, *Escherichia fergusonii, Bosea thiooxidans, Variovorax guangxiensis, Pseudomonas oryzihabitans, Agrobacterium tumefaciens, Simplicispira metamorpha, Serratia nematodiphila, Comamonas guangdongensis, Simplicispira* sp., *Methylobacterium phyllosphaerae, Microbacterium testaceum*, and *Enterobacter sichuanensis*. Isolates K2, K8, and K18 are potential as PGP, but % identity with GenBank is very low, respectively 79.75, 80.54, and 79.50%. The three isolates were obtained from roots and petiole cv. Klutuk and were unavailable in other organs (Table 6). Seeing its potential as PGPB and it is associated with cv. Klutuk, which is a resistant cultivar, requires further identification and characterization.

Interestingly, r_K2, r_K8, and r_K117 isolates had been proven can significantly improve the growth of tomato plant (Sidiq, et al., 2024).

Table 6. Number of isolates that displayed more than one plant growth-promoting trait

Isolate ID	Phylum /classes	Ordo	16S rRNA closest relative	% ident	A	B	C	D	E	F
r_K1	Proteobacteria/γ	Enterobacteriales	*Klebsiella grimontii* strain SB73	94.20	++	37.3	-	-	-	46
r_K2	Proteobacteria/γ	Enterobacteriales	-	**79.75**	+	73.5	-	31.6	1.12	44
r_K3	Proteobacteria/γ	Pseudomonadales	*Acinetobacter oryzae* strain B23 (T)	99.43	+	59.9	-	-	-	-
r_K7	Proteobacteria/γ	Enterobacteriales	*Pantoea* sp. strain CoA11	99.79	++	16.2	-	26.3	-	51
r_K8	Proteobacteria/γ	Enterobacteriales	-	**80.54**	+	59.5	-	29	1.3	45
r_K10	Proteobacteria/γ	Enterobacteriales	*Pseudescherichia vulneris* strain NBRC 102420	92.88	++	73.5	-	34.3	-	-
r_K14	Proteobacteria/γ	Enterobacteriales	*Pseudescherichia vulneris strain* NBRC 102420	93.69	++	58.2	-	29	1.33	-
p_K18	Firmicutes	Bacillales	-	**79.50**	-	-	-	-	-	54
p_K22	Firmicutes	Lactobacillales	*Bacillus kochii* strain WCC 4582	99.79	++	57.7	-	-	-	-
p_K25	Actinobacteria	Micrococcales	*Brachybacterium huguangmaarense* strain M1	97.91	++	62.9	-	-	-	-
r_K35	Proteobacteria/γ	Enterobacteriales	*Enterobacter cloacae* subsp. dissolvents strain LMG 2683(T)	100.00	+	59.8	-	30	-	-
p_K58a	Proteobacteria/α	Sphingomonadales	*Novosphingobium pokkalii* strain L3E4	99.78	+	5.8	-	26.1	-	48
r_K75	Proteobacteria/γ	Enterobacteriales	*Escherichia fergusonii* ATCC 35469	99.57	+	26.2	+	38.9	-	-
r_K86	Proteobacteria/α	Rhizobiales	*Bosea thiooxidans* strain BI-42	98.97	++	-	+	27.8	-	43
r_K111	Proteobacteria/β	Burkholderiales	*Variovorax guangxiensis* strain GXGD002	92.02	-	72.6	-	41.7	2.8	-
r_K114	Proteobacteria/γ	Pseudomonadales	*Pseudomonas oryzihabitans* strain NBRC 102199	99.57	+	-	+	44.4	2.67	-
r_K115	Proteobacteria/α	Rhizobiales	*Agrobacterium tumefaciens* strain IAM 12048	97.43	++	-	+	25	-	48
r_K117	Proteobacteria/β	Burkholderiales	*Simplicispira metamorpha* strain DSM 1837	90.47	+	42.6	+	44.4	-	44
r_K324	Proteobacteria/γ	Enterobacteriales	*Serratia nematodiphila* DZ0503SBS1	99.57	+	-	+	44.4	-	49
p_A9	Proteobacteria/β	Burkholderiales	*Comamonas guangdongensis* strain CY01	95.00	++	46.6	+	36.1	-	-
r_A22	Proteobacteria/γ	Enterobacteriales	*Pantoea dispersa* strain: DSM 30073	98.19	-	65.4	-	38.9	-	43
r_A24	Proteobacteria/γ	Enterobacteriales	*Pantoea endophytica* strain 596	99.48	+	-	-	36.1	2.72	-
p_A30	Proteobacteria/β	Burkholderiales	*Simplicispira* sp. CPCC 100842	97.22	++	44.2	+	30.6	2.1	33
c_A31	Proteobacteria/α	Rhizobiales	*Methylobacterium phyllosphaerae* strain CBMB27	92.88	++	-	+	27.8	-	41
c_A34	Proteobacteria/γ	Pseudomonadales	*Pseudomonas putida* strain JPR22	99.93	++	-	+	38.9	1.67	-
r_A41	Proteobacteria/α	Rhizobiales	*Beijerinckia fluminensis* strain UQM 1685	99.63	++	44.6	-	-	0.83	-
r_A44b	Actinobacteria	Micrococcales	*Microbacterium testaceum* strain DSM 20166	99.00	++	31.1	+	-	0.17	46
r_A50	Proteobacteria/γ	Enterobacteriales	*Erwinia tasmaniensis* Et1/99	98.01	++	10.8	-	-	-	50
r_A51	Proteobacteria/γ	Enterobacteriales	*Enterobacter sichuanensis*	99.29	+	68	+	-	-	49

Note: A: N fixation (+, ++, or -), B: IAA production (ppm), C: ACC deaminase activity (+ or -), D: siderophore production >25%, E: PO4 solubilization (index), F: antifungal activity against Foc (%). ID isolates column: letter r: root, p: petiole, c: corm; the letter after the "_" K: cv. Klutuk, A: cv. Ambon. The next number shows the isolate number. Positive (+); strongly positive (++); negative (-)

These species are Phylum Proteobacteria except *Bacillus* (p. Firmicutes), *Microbacterium*, and *Brachybacterium* (p. Actinobacteria). *Pseudomonas* and *Bacillus* show promising biocontrol characteristics (Santoyo et al. 2012). *Pantoea* also contributes to the host plant's ability to withstand drought stress (Chen et al. 2017) and high salinity (Sun et al. 2020). *Microbacterium*, which is an actinobacterium, is reported as a potential endophyte as PGP, including its ability to respond to drought stress (Govindasamy et al. 2020), while *Simplicispira* still has not many reports of its ability as PGPB.

Moreover, to select the potential of endophytic bacteria as PGP, the character of IAA production is considered the most essential. The IAA-producing bacteria will colonize the roots better than other bacteria; IAA will soften the host cell wall at certain concentrations, increasing root exudate and becoming an attractant for rhizosphere bacteria (Etesami and Alikhani 2015). IAA from these bacteria also plays a role in stimulating the development of the root system of the host to increase the absorption of nutrients such as Fe and P. With a developing root system, plants will be able to cope with stress, especially against drought (Etesami and Alikhani 2015). Additionally, cv. Klutuk is a resistant cultivar; this IAA-producing endophytic bacteria plays a role in this resistance property.

Organs of banana plants and characteristics of bacterial isolates as PGP

Isolates obtained from root organs had the most PGP characters, followed by isolates obtained from petiole, and the last one was isolates obtained from corms. Such a pattern appears in cv. Klutuk and cv. Ambon, which grows on different soils (Table 4). Endophytic bacteria such as PGP were dominated by Phylum Proteobacteria (Gamma, Alpha, Beta), followed by Firmicutes and Actinobacteria. Isolates, including Gammaproteobacteria, dominated almost all samples. The sequence of the dominant order is Pseudomonadales (c. Gammaproteobacteria), Enterobacteriales (c. Gammaproteobacteria), and Bacillales (p. Firmicutes). The next sequence is Rhizobiales (c. Alphaproteobacteria), Burkholderiales (c. Betaproteobacteria), Lactobacilalles (p. Firmicutes), and Micrococcales (p. Actinobacteria) and other orders such as Sphingomonadales (c. Alphaproteobacteria), Gomonadales (c. Alphaproteobacteria), Flavobacteriales (p. Bacteriodetes) (Table 8).

The genus *Acinetobacter* seemed to dominate the characters capable of binding N, IAA production, PO_4 solubilization, and antifungal activity against Foc. *Pseudomonas* dominates the characters capable of binding N, ACC deaminase activity, siderophore production, and antifungal activity against Foc. *Bacillus, Enterobacter*, *Simplicispira*, and *Pantoea* also appear to have characters capable of binding N, siderophore production, and antifungal activity against Foc. The genus *Agrobacterium*, *Pantoea*, and *Variovorax* have siderophore production characters, while the PO_4 solubilization characters are dominated by the genus *Acinetobacter*. For antifungal activity against Foc, there are 6 dominant genera, namely *Acinetobacter, Enterobacter, Klebsiella, Pantoea, Rhizobium*, and *Simplicispira* (Table 7).

Table 7. Number of genera that have characters as PGP

Genera	Number of genera members showing each PGP character						Total
	a	**b**	**c**	**d**	**e**	**f**	
Acidovorax	1	0	0	1	0	0	2
Acinetobacter	12	6	1	2	15	2	38
Aeromonas	2	0	1	1	1	0	5
Agrobacterium	4	0	1	4	0	1	10
Arthrobacter	1	0	0	1	0	0	2
Bacillus	6	1	0	6	1	1	15
Beijerinckia	2	2	1	1	1	1	8
Bosea	2	0	1	1	0	1	5
Brachybacterium	2	1	0	0	0	0	3
Brevibacterium	1	0	0	1	0	1	3
Citrobacter	1	1	0	1	1	1	5
Comamonas	1	1	1	1	0	0	4
Chryseobacterium	0	1	0	0	0	0	1
Dickeya	1	0	0	1	0	0	2
Enterobacter	4	2	2	2	0	2	12
Erwinia	1	0	0	0	0	1	2
Escherichia	1	0	1	1	0	0	3
Herbaspirillum	0	0	0	2	0	1	3
Klebsiella	2	0	0	0	1	2	5
Kluyvera	1	1	0	1	1	1	5
Methylobacterium	2	1	2	1	0	0	6
Microbacterium	2	3	1	3	1	1	11
Micrococcus	0	0	0	1	1	0	2
Moraxella	2	1	0	1	0	0	4
Mycobacterium	1	0	0	0	1	0	2
Novosphingobium	4	1	1	2	0	1	9
Oceanobacillus	0	0	0	0	0	1	1
Paenibacillus	1	1	0	1	0	0	3
Pantoea	3	3	1	4	1	2	14
Pseudacidovorax	2	3	0	1	1	0	7
Pseudescherichia	2	2	0	2	1	0	7
Pseudomonas	12	3	5	7	3	0	30
Rhizobium	1	1	0	0	0	2	4
Rothia	0	0	0	0	1	0	1
Salinicoccus	2	0	0	0	0	0	2
Scandinavium	0	1	0	0	0	0	1
Serratia	1	0	1	1	0	1	4
Shigella	1	0	0	1	1	0	3
Simplicispira	6	2	3	2	0	2	15
Sphingomonas	1	0	0	0	0	0	1
Staphylococcus	0	0	1	1	0	0	2
Stenotrophomonas	1	0	0	1	0	0	2
Terribacillus	1	1	0	1	0	0	3
Variovorax	2	1	1	3	2	1	10

Note: IAA production (ppm), ACC deaminase activity (+/-), Siderophore production (>25 %), PO_4 Solubilization Index, Antifungal activity against FoC (%)

Table 8. Endophytic bacteria have the character of PGPB based on the plant organs of the two banana cultivars at the phylum-to-order levels

Phylum	Classes	Ordo	Klutuk			Ambon			Total
			R	P	C	R	P	C	
Proteobacteria	Gamma	Pseudomonadales	14	9	1	4	2	4	34
		Enterobacteriales	13	1	0	9	0	1	24
		Xanthomonadales	1	0	0	0	0	0	1
		Aeromonadales	0	0	0	1	0	2	3
	Beta	Burkholderiales	6	1	0	1	3	0	11
	Alpha	Rhizobiales	7	3	1	2	0	2	15
		Sphingomonadales	2	3	1	0	0	0	6
Firmicutes		Bacillales	1	2	1	2	0	0	6
		Lactobacillales	1	6	2	1	2	1	13
Actinobacteria		Micrococcales	1	6	1	2	0	0	10
		Corynebacteriales	0	0	0	1	0	0	1
Bacteriodetes		Flavobacteriales	1	0	0	0	0	0	1
Total			47	31	7	23	7	10	**125**

Note: R: root; P: petiole; C: corm

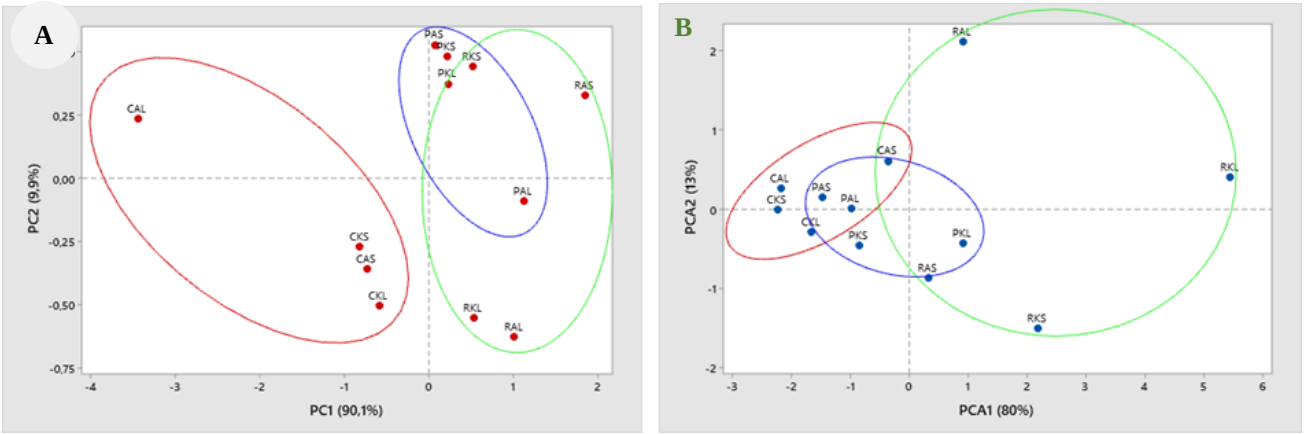

Figure 2. Principal component analysis (PCA) of (A.) endophytic bacterial population (CFU/g tissue) and (B.) characters as PGPB (N fixation, IAA production, ACC deaminase activity, siderophore production, PO4 solubilization, and antifungal activity against Foc. Legend: plant organ samples (R: root, C: corm, P: petiole), banana cultivars (K: Klutuk, A: Ambon), and soil types (L: Loamy sandy/LS, S: Silt loamy/SL)

PCA showed that the endophytic bacterial population and its character as PGP were influenced by plant organs but not by plant cultivars and soil types. Figure 2.A shows that the sample of corm formed a separate group from petiole and root, even though the RKS and PAL samples were separate from the group. For the characteristic of endophytic bacteria as PGP, samples from corm, petiole, and root formed groups even though the CAS and PKL samples separated from the group (Figure 2.B). The overlapping species among the organs, cultivars, and soil types could cause their separation. Separation of RKS, PAL, CAS, and PKL samples indicated the sharing of bacterial species inside the root, corm, and petiole organs, silt and sandy soil types, and banana cultivars. Nevertheless, it was clear that the plant organ was the most influential to the bacterial community as well as the PGP characters.

Additionally, two different types of soils did not classify the endophytic bacteria in a certain group. Thus, soil type did not affect the endophytic bacterial community in banana cultivars. A report stated that the soil pH, vegetation type, and plant diversity affected the bacterial community inside the soil (Cheng et al. 2020). Oppositely, the balance bacterial community affected the physicochemical properties of soils (He et al. 2023). However, the effect of soil type on the endophytic bacterial community inside the plants is limitedly known. Soil types are strong but variably influencing the plant seedling bacteriome (Walsh et al. 2021). Non-affecting soil type to the endophytic bacterial community in banana plants in this study might be caused by relatively similar physicochemical properties of the two soil types (Table 1).

In conclusion, the colonization of endophytic bacteria with multiple plant growth-promoting (PGP) traits varies across different plant organs. Specifically, both roots and petioles harbor endophytic bacterial populations in banana plants. Notably, certain isolates from the cv. Klutuk

appears to represent a potential new species with promising PGP capabilities, which were not observed in the cv. Ambon.

ACKNOWLEDGEMENTS

This research was supported by the Ministry of Research, Technology, and Higher Education, Republic of Indonesia, by Doctoral Dissertation Research, No. 2125/ UN1./DITLIT/DIT-LIT/PT/2020. We would also like to thank Miftahussurur, for supporting the data analysis.

REFERENCES

Aini LQ, Trianti I, Rachmawati SW, Putra AM, Anastasya NA, Setiawan A. 2023. In vitro characterization of UB Forest (Malang, Indonesia) indigenous bacteria as plant growth promoting bacteria (PGPB). Biodiversitas 24 (8): 4558-4565. DOI: 10.13057/biodiv/d240837.

Ali SZ, Sandhya V, Rao LV. 2014. Isolation and characterization of drought-tolerant ACC deaminase and exopolysaccharide-producing fluorescent *Pseudomonas* sp. Ann Microbiol 64: 493-502. DOI: 10.1007/s13213-013-0680-3.

Andrade LF, de Souza GL, Nietsche S, Xavier AA, Costa MR, Cardoso AM, Pereira MC, Pereira DF. 2014. Analysis of the abilities of endophytic bacteria associated with banana tree roots to promote plant growth. J Microbiol 52: 27-34. DOI: 10.1007/s12275-014-3019-2.

Arora NK, Verma M. 2017. Modified microplate method for rapid and efficient estimation of siderophore produced by bacteria. 3 Biotech 7: 1-9. DOI: 10.1007/s13205-017-1008-y.

Bigot S, Salcedo SP. 2017. The influence of two-partner secretion systems on the virulence of *Acinetobacter baumannii*. Virulence 8 (6): 653-654. DOI: 10.1080/21505594.2017.1283465.

Chen Y, Fan J, Du L, Xu H, Zhang Q, He Y. 2014. The application of phosphate solubilizing endophyte *Pantoea dispersa* triggers the microbial community in red acidic soil. Appl Soil Ecol 84: 235-244. DOI: 10.1016/j.apsoil.2014.05.014.

Cheng J, Zhao M, Cong J, Qi Q, Xiao Y, Cong W, Deng Y, Zhou J, Zhang Y. 2020. Soil pH exerts stronger impacts than vegetation type and plant diversity on soil bacterial community composition in subtropical broad-leaved forests. Plant Soil 450: 273-286. 10.1007/s11104-020-04507-2.

Coleman-Derr D, Desgarennes D, Fonseca-Garcia C, Gross S, Clingenpeel S, Woyke T, North G, Visel A, Partida-Martinez L, Tringe S. 2015. Plant compartment and biogeography affect microbiome composition in cultivated and native Agave species. New Phytol 209 (2): 798-811. DOI: 10.1111/nph.13697.

de Fretes CE, Suryani R, Purwestri YA, Nuringtyas TR, Widianto D. 2018. Diversity of endophytic bacteria in sweet sorghum (*Sorghum bicolor* (L.) Moench) and their potential for promoting plant growth. Indian J Sci Technol 11 (11): 1-10. DOI: 10.17485/ijst/2018/v11i11/120283.

Djatmiko HA, Prihatiningsih N, Lestari P. 2023. Bioprospection of single and a consortium endophytic bacteria of suboptimal field rice isolates as biocontrol of rice bacterial leaf blight pathogens. Biodiversitas 24 (5): 2710-2715. DOI: 10.13057/biodiv/d240524.

Etesami H, Alikhani HA, Hosseini HM. 2015. Indole-3-acetic acid (IAA) production trait, a useful screening to select endophytic and rhizosphere competent bacteria for rice growth promoting agents. MethodsX 2: 72-78. DOI: 10.1016/j.mex.2015.02.008.

Galindo-Castañeda T, Brown KM, Kuldau GA, Roth GW, Wenner NG, Ray S, Schneider H, Lynch JP. 2019. Root cortical anatomy is associated with differential pathogenic and symbiotic fungal colonization in maize. Plant Cell Environ 42 (11): 2999-3014. DOI: 10.1111/pce.13615.

Govindasamy V, George P, Kumar M, Aher L, Raina SK, Rane J, Annapurna K, Minhas PS. 2020. Multi-trait PGP rhizobacterial endophytes alleviate drought stress in a senescent genotype of sorghum [*Sorghum bicolor* (L.) Moench]. 3 Biotech 10 (1): 1-14. DOI: 10.1007/s13205-019-2001-4.

Green ER, Mecsas J. 2016. Bacterial secretion systems: An overview. Microbiol Spectrom 4 (10): 1128. DOI: 10.1128/microbiolspec.vmbf-0012-2015.

Hamane S, El YemLahi A, Zerrouk MH, El Galiou O, Laglaoui A, Bakkali M, Arakrak A. 2023. Plant growth promotion and biocontrol potentiality of endophytes isolated from Root nodules of *Sulla flexuosa* L. plants. Intl J Agron 2023: 1-9. DOI: 10.1155/2023/2451806.

Harding CM, Hennon SW, Feldman MF. 2017. Uncovering the mechanisms of *Acinetobacter baumannii* virulence. Nat Rev Microbiol 16 (2): 91-102. DOI: 10.1038/nrmicro.2017.148.

He C, Li K, Wen C, Li J, Fan P, Ruan Y, Meng L, Jia Z. 2023. Changes in physicochemical properties and bacterial communities of tropical soil in china under different soil utilization types. Agronomy 13: 1897. DOI: 10.3390/agronomy13071897.

Hernandez RE, Gallegos-Monterrosa R, Coulthurst SJ. 2020. Type VI secretion system effector proteins: Effective weapons for bacterial competitiveness. Cell Microbiol 22 (9): e13241. DOI: 10.1111/cmi.13241.

Hölscher D, Buerkert A, Schneider B. 2016. Phenylphenalenones accumulate in plant tissues of two banana cultivars in response to herbivory by the banana weevil and banana stem weevil. Plants 5 (3): 34. DOI: 10.3390/plants5030034.

Horna, G, Ruiz J. 2021. Type 3 secretion system of *Pseudomonas aeruginosa*. Microbiol Res 246: 126719. DOI: 10.1016/j.micres.2021.126719.

Kallow S, Longin K, Sleziak NF, Janssens SB, Vandelook F, Dickie J, Swennen RL, Paofa J, Carpentier SC, Panis B. 2020. Challenges for ex situ conservation of wild bananas: Seeds collected in Papua New Guinea have variable levels of desiccation tolerance. Plants 9 (9): 1243. DOI: 10.3390/plants9091243.

Kara M, Soylu S. 2022. Isolation of endophytic bacterial isolates from healthy banana trees and determination of their in vitro antagonistic activities against crown rot disease agent *Fusarium verticillioides*. MKU. J Agric Sci 27 (1): 36-46. DOI: 10.37908/mkutbd.102134.

Karthik M, Pushpakanth P, Krishnamoorthy R, Senthilkumar M. 2017. Endophytic bacteria associated with banana cultivars and their inoculation effect on plant growth. J Hortic Sci Biotechnol 92 (6): 568-576. DOI: 10.1080/14620316.2017.1310600.

Kaushal M, Swennen R, Mahuku G. 2020. Unlocking the microbiome communities of banana (*Musa* spp.) under disease stressed (fusarium wilt) and non-stressed conditions. Microorganisms 8 (3): 443. DOI: 10.3390/microorganisms8030443.

Kissel E, van Asten, Swennen R, Lorenzen J, Carpentier SC. 2015. Transpiration Efficiency versus growth: Exploring the banana biodiversity for drought tolerance. Sci Hortic 185: 175-182. DOI: 10.1016/j.scienta.2015.01.035.

Köberl M, Dita M, Martinuz A, Staver C, Berg G. 2017. Members of Gammaproteobacteria as indicator species of healthy banana plants on Fusarium wilt-infested fields in Central America. Sci Rep 7: 1-9. DOI: 10.1038/srep45318.

Köberl M, Dita M, Nimusiima J, Tumuhairwe JB, Kubiriba J, Staver C, Berg G. 2018. The banana microbiome: Stability and potential health indicators. Acta Hortic 1196: 1-8. DOI: 10.17660/actahortic.2018.1196.1.

Kumar A, Droby S, Singh VK, Singh SK, White JF. 2020. Entry, colonization, and distribution of endophytic microorganisms in plants. In Microbial endophytes (pp. 1-33). Woodhead Publishing. DOI: 10.1016/B978-0-12-819654-0.00001-6.

Lewis JM, Deveson-Lucas D, Harper M, Boyce JD. 2019. Systematic identification and analysis of *Acinetobacter baumannii* type VI secretion system effector and immunity components. Front Microbiol 10: 2440. DOI: 10.3389/fmicb.2019.02440.

Li C, Yang J, Li W, Sun J, Peng M. 2017. Direct root penetration and rhizome vascular colonization by *Fusarium oxysporum* f. sp. *cubense* are the key steps in the successful infection of Brazil cavendish. Plant Dis 101: 2073-2078. DOI: 10.1094/pdis-04-17-0467-re.

Liu H, Carvalhais LC, Crawford M, Singh E, Dennis PG, Pieterse CMJ and Schenk PM. 2017. Inner Plant Values: Diversity, Colonization and Benefits from Endophytic Bacteria. Front Microbiol 8: 2552. DOI: 10.3389/fmicb.2017.02552

Lovecká P, Kroneislová G, Novotná Z, Röderová J, Demnerová K. 2023. Plant growth-promoting endophytic bacteria isolated from *Miscanthus giganteus* and their antifungal activity. Microorganisms 11 (11): 2710-2710. DOI: 10.3390/microorganisms11112710.

Marcano I, Diaz-Alcantara C, Cesar-Antonia, Urbano B, Gonzalez-Andres F. 2016. Assessment of bacterial populations associated with banana tree roots and development of successful plant probiotics for banana crop. Soil Biol Biochem 99: 1-20. DOI: 10.1016/j.soilbio.2016.04.013.

Maryani N, Lombard L, Poerba YS, Subandiyah S, Crous PW, Kema GHJ. 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. DOI: 10.1016/j.simyco.2018.06.003.

Matos AMD, Gomes ICP, Nietsche S, Xavier AA. 2017. Phosphate solubilization by endophytic bacteria isolated from banana trees. An Acad Bras Cienc 89 (04): 2945-2954. DOI: 10.1590/0001-3765201720160111.

Meliani A, Bensoltane A, Benidire L, Oufdou K. 2017. Plant growth-promotion and IAA secretion with *Pseudomonas fluorescens* and *Pseudomonas putida*. Res Rev: J Bot Sci 6: 16-224.

Miliute I, Buzaite O, Baniulis D, Stanys V. 2015. Bacterial endophytes in agricultural crops and their role in stress tolerance: A Review. Zemdirbyste-Agric 102 (4): 465-478. DOI: 10.13080/z-a.2015.102.060.

Nurbailis N, Yanti Y, Resti Z, Djamaan A, Rahayu SD. 2023. Consortia of endophytic bacteria for controlling *Colletotrichum gloeosporiodes* causing anthracnose disease in chili plant. Biodiversitas 24 (6): 3503-3511. DOI: 10.13057/biodiv/d240648.

Patel P, Shah R, Modi K. 2017. Isolation and characterization of plant growth promoting potential of *Acinetobacter* sp. RSC7 isolated from *Saccharum officinarum* cultivar Co 671. J Exp Biol Agric Sci 5 (4): 483-491. DOI: 10.18006/2017.5(4).483.491.

Paul D, Sinha SN. 2017. Isolation and characterization of phosphate solubilizing bacterium *Pseudomonas aeruginosa* KUPSB12 with antibacterial potential from river Ganga, India. Ann Agrarian Sci 15 (1): 130-136. DOI: 10.1016/j.aasci.2016.10.001.

Pinski A, Betekhtin A, Hupert-Kocurek K, Mur LAJ, Hasterok R. 2019. Defining the genetic basis of plant-endophytic bacteria interactions. Intl J Mol Sci 20 (8): 1947. DOI: 10.3390/ijms20081947.

Ploetz RC. 2015. Fusarium wilt of banana. Phytopathology 105: 1512-1521. DOI: 10.1094/phyto-04-15-0101-rvw.

Prieto A, Möder M, Rodil R, Adrian L, Marco-Urrea E. 2011. Degradation of the antibiotics norfloxacin and ciprofloxacin by a white-rot fungus and identification of degradation products. Bioresour Technol 102 (23): 10987-10995. DOI: 10.1016/j.biortech.2011.08.055.

Ragavi G, Muthamilan M, Nakkeeran S, Kumaravadivel N, Sivakumar U, Suganthi A. 2019. Phenotypic and molecular characterization of endophytic bacteria isolated from banana. Curr J Appl Sci Technol 38 (6): 1-10. DOI: 10.9734/cjast/2019/v38i630402.

Rahayu T, Purwestri YA, Subandiyah S, Suparmin A, Widianto D. 2021. Exploration of core endophytic bacteria from different organs of diploid *Musa balbisiana* and triploid *Musa acuminata*. Agric Natural Resour 55 (5): 787-794. DOI: 10.34044/j.anres.2021.55.5.09.

Rahayu T, Suparti S, Widyayanti S, Kristamtini, K, Sidiq Y. 2023. Endophytic bacteria from banana plant improves the growth and yield of black rice plant. SABRAO J Breed Genet 55 (3): 951-964. DOI: 10.54910/sabrao2023.55.3.29.

Ravi I, Uma S, Vaganan MM, Mustaffa MM. 2013. Phenotyping bananas for drought resistance. Front Physiol 4: 9. DOI: 10.3389/fphys.2013.00009.

Repizo GD. 2017. Prevalence of *Acinetobacter baumannii* strains expressing the Type 6 secretion system in patients with bacteremia. Virulence 8: 1099-1101. DOI: 10.1080/21505594.2017.1346768.

Robinson JC, Saúco VG. 2010. Bananas and plantains (Vol. 19). Cabi, UK.

Sachdev D, Nema P, Dhakephalkar P, Zinjarde S, Chopade B. 2010. Assessment of 16S rRNA gene-based phylogenetic diversity and promising plant growth-promoting traits of Acinetobacter community from the rhizosphere of wheat. Microbiol Res 165 (8): 627-638. DOI: 10.1016/j.micres.2009.12.002.

Samaddar S, Chatterjee P, Choudhury R, Ahmed S, Sa T. 2019. Interactions between *Pseudomonas* spp. and their role in improving the red pepper plant growth under salinity stress. Microbiol Res 219: 66-73. DOI: 10.1016/j.micres.2018.11.005.

Santoyo G, Moreno-Hagelsieb G, del Carmen Orozco-Mosqueda M, Glick BR. 2016. Plant growth-promoting bacterial endophytes. Microbiol Res 183: 92-99. DOI: 10.1016/j.micres.2015.11.008.

Sekhar AC, Thomas P. 2015. Isolation and identification of shoot-tip associated endophytic bacteria from banana cv. grand naine and testing for antagonistic activity against *Fusarium oxysporum* f. sp. *cubense*. Am J Plant Sci 6: 943-954. DOI: 10.4236/ajps.2015.67101.

Sidiq Y, Assyifa AN, Rahayu T, Mumpuni KE. 2024. Endophytic Bacteria Improves the Growth of Tomato Plants: An Initial Trial Towards Sustainable Agriculture. IOP Conf Ser Earth Environ Sci 1357: 012015. DOI: 10.1088/1755-1315/1357/1/012015

Souza GLOD, Nietsche S, Xavier AA, Costa MR, Pereira MCT, Santos MA. 2016. Triple combinations with PGPB stimulate plant growth in micropropagated banana plantlets. Appl Soil Ecol 103: 31-35. DOI: 10.1016/j.apsoil.2016.03.001.

Sumardi I, Wulandari M. 2010. Anatomy and morphology character of five Indonesian banana cultivars (*Musa* spp.) of different ploidy level. Biodiversitas 11 (4): 167-175. DOI: 10.13057/biodiv/d110401.

Sun L, Lei P, Wang Q, Ma J, Zhan Y, Jiang K, Xu Z, Xu H. 2020. The endophyte pantoea alhagi nx-11 alleviates salt stress damage to rice seedlings by secreting exopolysaccharides. Front Microbiol 10: 1-13. DOI: 10.3389/fmicb.2019.03112.

Sunandar A. 2017. New record of wild banana (*Musa balbisiana* Colla) in West Kalimantan, Indonesia. Biodiversitas 18: 1324-1330. DOI: 10.13057/biodiv/d180406.

Sutio G, Iskandar I, Indriyati LT, Djajakirana G. 2023. Effectiveness of potassium humate and endophytic bacteria from *Serratia marcescens* strain NPKC3_2_21 in increasing root weight of paddy cultivation in acidic soil. Biodiversitas 24 (11): 6316-6322. DOI: 10.13057/biodiv/d241156.

Thangavelu MR, Gopi M. 2015. Field suppression of Fusarium wilt disease in banana by the combined application of native endophytic and rhizospheric bacterial isolates possessing multiple functions. Phytopathol Mediterr 54: 241-252. DOI: 10.14601/Phytopathol_Mediterr-15160.

Thomas P, Soly TA. 2009. Endophytic bacteria associated with growing shoot tips of banana (*Musa* sp.) cv. Grand Naine and the affinity of endophytes to the host. Microb Ecol 58: 952-964. DOI: 10.1007/s00248-009-9559-z.

Tripathi L, Tripathi JN, Shah T, Muiruri KS, Katari M. 2019. Molecular basis of disease resistance in banana progenitor *Musa balbisiana* against *Xanthomonas campestris* pv. *musacearum*. Sci Rep 9: 7007. DOI: 10.1038/s41598-019-43421-1.

Vaidya H, Kapadia C, Borse B, Vyas TK, Patel N. 2021. Diverse novel bacterial endosymbionts and their plant growth promoting traits in association with banana plant. Intl J Curr Microbiol Appl Sci 10 (2): 2047-2059. DOI: 10.20546/ijcmas.2021.1002.244.

Vanhove AC, Vermaelen W, Panis B, Swennen R, Carpentier SC. 2012. Screening the banana biodiversity for drought tolerance: Can an in vitro growth model and proteomics be used as a tool to discover tolerant varieties and understand homeostasis. Front Plant Sci 3: 176. DOI: 10.3389/fpls.2012.00176.

Walsh CM, Becker-Uncapher I, Carlson M, Fierer N. 2021. Variable influences of soil and seed-associated bacterial communities on the assembly of seedling microbiomes. ISME J 15 (9): 2748-2762. DOI: 10.1038/s41396-021-00967-1.

Wang Y, Yang C, Yao Y, Wang Y, Zhang Z, Xue L. 2016. The diversity and potential function of endophytic bacteria isolated from *Kobreasia capillifolia* at Alpine grasslands on the Tibetan Plateau, China. J Integr Agric 15: 2153-2162. DOI: 10.1016/s2095-3119(15)61248-5.

Warman NM, Aitken EAB. 2018. The movement of *Fusarium oxysporum* f.sp. Cubense (sub-tropical race 4) in susceptible cultivars of banana. Front Plant Sci 871: 1-9. DOI: 10.3389/fpls.2018.01748.

Wei L, Yang C, Cui L, Jin M, Osei R. 2023. *Bacillus spp*. isolated from pepper leaves and their function and inhibition of the fungal plant pathogen *Colletotrichum scovillei*. Egypt J Biol Pest Control 33 (1): 46. DOI: 10.1186/s41938-023-00686-z.

Zhao A, Ding X, Huang M, Cheng Y. 2023. Bioprospecting plant-growth-promoting endophytic bacteria isolated from moso bamboo (*Phyllostachys edulis*) shoots. Forests 14 (10): 2061-2061. DOI: 10.3390/f14102061.

Zhao G, Zhu X, Zheng G, Meng G, Dong Z, Baek JH, Jeon CO, Yao Y, Xuan YH, Zhang J, Jia B. 2024. Development of biofertilizers for sustainable agriculture over four decades (1980-2022). Geogr Sustain 5 (1): 19-28. DOI: 10.1016/j.geosus.2023.09.006.