

Impact of *Paenibacillus polymyxa* Amendment on Soil Bacterial Communities and Physicochemical Properties in Sandy Soil Restoration

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ABSTRACT

Soil infertility is a significant challenge in achieving sustainable agricultural practices. In this regard, the chemical fertilizer usage is not an environmentally friendly solution. Organic amendment and bacterial inoculation can positively restore soil quality, enhancing biogeochemical nutrient cycles. In this study, we assessed the effect of adding plant growth-promoting bacteria (PGPB) alongside organic amendments on the physicochemical parameters of sandy-loam soils. Over a 90-day pot experiment, we measured organic matter accumulation, physicochemical, chemical variation trends and changes in microbial community assemblages. Working on the joint application could have a synergistic effect; different agro wastes spent such as mushroom substrate (SMS), empty fruit bunch (EFB) of palm oil and pineapple leaf (PL) residue was amended with *Paenibacillus polymyxa* ATCC 825 and effective microorganism. Significant changes in soil properties (physicochemical and microbial community) due to the application of *P. polymyxa* and SMS-amended material

were observed after incubation. On average, an increase in water holding capacity, soil pH and mineral content availability was significantly higher than other amended materials. Compared to others, the organic amendment significantly increased sandy-soil aggregation content by 44%. In addition, increased taxonomic diversity in phyla composition was observed with an abundance of *Proteobacteria* (33%), *Firmicutes* (18%), *Actinobacteria* (14%), *Bacteroidata* (12%), and *Verrucomicrobia* (6%). The findings indicate that the addition of SMS amendment

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with bacterial inoculation is beneficial for problematic soil recovery. The incorporation of bacterial inoculation, specifically *P. polymyxa* ATCC 825, following organic amendment, seems to have a greater positive effect on the soil characteristics

Keywords: Agro-waste, microbial community structure, organic amendment, *Paenibacillus polymyxa*, sandy soil

INTRODUCTION

Land desertification is a worldwide issue receiving much attention nowadays, affecting the socio-economic and ecological environment. Unsuitable agricultural practices and anthropogenic activities have resulted in permanent soil fertility degradation. This frequently degraded soil is characterized by decreasing levels of soil organic matter and low fertility as consequences of intensive land use. Generally, sandy soils contain much lower carbon content, high evapotranspiration and poor aggregate stability with coarse-loose particle structure, influencing their water retention and adhesion to any mineral elements (Vityakon, 2007; Herawati et al., 2020). Sandy soil covers 86,000 km² in Asia, and that region is not suitable for cropping purposes. In comparison with other soils, tropical sandy soil tends to possess low storage of C content and is presumed to be very fragile to mitigate greenhouse gas (GHG) emissions (Arunrat et al., 2020). As a result, the ecosystem functioning of desertified land is likely unstable, restricting its reclamation to normal conditions. Therefore, the realization of resource utilization for sandy soil restoration offers great significance to reducing soil depletion while achieving environmental protection.

An important step for soil restoration is the identification of feasible amendment strategies. In this regard, the organic amendment seems feasible and practical as the efficacies of physical and chemical methods are doubtly questioned in terms of safety and cost implication (Sahin et al., 2011; Singh et al., 2016). In light of the role played by organic amendment, it is vital to consider this approach as it has been proven to improve aggregate stability and soil organic content (SOC). SOC plays an important indicator in evaluating soil aggregate stability. It is primarily due to increased organic matter content that promotes the proliferation of soil microbial community diversity through decomposition and mineralization processes (Kamolmanit et al., 2013). Having a significant impact on the microbial structure, Tang et al. (2015) demonstrated that organic carbon content has a high correlation with soil respiration rate, with an increase in microbial diversity, thus promoting aggregate formation. The application of organic inputs with good biochemical quality is considered feasible as a means of guaranteeing SOC accumulation in the sandy soil. According to Putasso et al. (2011), organic input with high N content and low cellulose and polyphenol content (tamarind residue) was a suitable option for amendment purposes under long-term field experiments in Thailand as soil stabilization was greatly regulated.

Much work has been conducted on the application of spent mushroom substrate (SMS) or any agro-waste to improve soil aggregate stability, as SMS can act as a cementing agent and composted material (Atallah et al., 2021; Loganathan et al., 2023). Specifically, spent mushroom compost (SMC) applies to establishing weak-structured and physically degraded soil. This positive result was attributed to the high level of organic carbon content and low-strength material properties (Gümüş & Şeker, 2017). The substantial addition of organic amendment input material increases SOC content per se and provides a readily available substrate for soil microbiome.

Native bacteria play an important role in maintaining soil fertility by mineralizing essential nutrients through solubilization and improving nutrient uptake. The application of microbial inoculants consisting of plant growth-promoting bacteria (PGPB) may enhance the mobility of low nutrient supply such as potassium and phosphorus. Following that, a relatively less explored bacterial strain, *Paenibacillus polymyxa*, was reported to have been intrinsically stable and capable of solubilizing phosphorus under extreme conditions (Mohd Din et al., 2020). Besides, a wealth of hydrolytic enzymes avenue together with exopolysaccharides (EPSs) capability from *P. polymyxa* has been reviewed by Daud et al. (2019) to mark the beneficial properties owned by that bacterial strain. In recent years, some scholars have researched the combined effect of microbial inoculation and organic amendment under semiarid conditions. For example, Mengual et al. (2014) have reported that using native rhizobacteria (*Bacillus megaterium* and *Bacillus* sp.) and composted sugar beet residue for soil rehabilitation showed a significant increase in phosphorus availability in the soil as compared to the control. Trivedi et al. (2017) have reported that microbial application has a positive effect on saline-sodic soil fertility with increased harvestable yield after amended soil incubation.

In Malaysia, sandy loam soils with a high volume of sand compared to silt are commonly often improved by organic amendment (Garbowski et al., 2023; Manickam et al., 2015). Additionally, 168 million tons of abundant agro-waste biomass generated from Malaysian agriculture systems have provided a good advantage in the exploitation route into a source of wealth. To elucidate the effect of different organic inputs (spent mushroom substrate [SMS], empty fruit bunch [EFB], pineapple leaf [PL] residues) amended with PGP bacteria on the physicochemical properties of sandy loam soil, we conducted a short-term experiment to quickly observe how these biochemically contrasting organic inputs lead to distinct shifts in microbial community structure and abundance. This study aims to test our hypothesis that increases in soil physicochemical properties are correlated with the selection of various organic materials used in conjunction with the microorganisms studied. Results from this study could provide an empirical solution in using the combination of PGPB and organic residues while minimizing environmental waste for application in a degraded sandy soil area.

MATERIALS AND METHODS

Experimental Site

Soil for our study was collected from the University of Technology Malaysia (UTM) research farm located in Pagoh province, southern state Johor, Malaysia (2°09'19.9"N 102°44'00.2"E) at an average altitude of 22 meters or 72.18 feet above sea level. The soil was taken from a depth of 20 cm. The area has a typically rain-fed attribute throughout the year. The average temperature is 32°C (<28°C minimum and about 40°C maximum). A hydrometer test was used to calculate the fraction of sand, silt, and clay in the soil and determine the texture of the soil using the US Department of Agriculture (USDA) triangle (Barman & Choudhury, 2020). The initial physicochemical properties of the collected soil sample are shown in Table 1. The texture of the soil was classified as sandy-loam soil with proportions: sand: 83%, silt: 9%, and clay: 8%, respectively. The soil used in this study has low aggregate stability and low organic matter content. Different organic inputs were used in this study, namely spent mushroom substrate (SMS), empty fruit bunch (EFB) of palm oil and pineapple leaf (PL) residues.

Table 1
Physiochemical properties of sandy-loam soil used in this study

Parameters	Sandy-loam soil (before treatment)
Moisture content (%)	35.0
pH	3.8
EC (dSm ⁻¹)	64.3
C/N ratio	0.4
Available P (mg kg ⁻¹)	29.2
Available K (mg kg ⁻¹)	399.8

Note. EC=Electrical conductivity; C/N ratio=Carbon to Nitrogen ratio; Available P= Available Phosphorus; Available K=Available Potassium

Experimental Design

The experiment involved different types of soil amendments and was conducted under greenhouse conditions (30°C ± 3). The experiment was arranged in a completely randomized design (CRD) with three replicates for each treatment. The air-dried and ground sandy soil was sieved to pass through a 2-mm sieve, and a total of 2 kg sieved soil was used for each treatment and placed in the pots (size 16' x 16') before being mixed with organic input materials. The effect of inoculant *P. polymyxa* ATCC 825 and Effective Microorganism (EM) applied on each of the organic inputs was assessed on organic matter accumulation, nutrient availability, acidity, water retention and soil aggregation of sandy-loam soil. All the treatments were mixed up with sandy soil in three replicates. Six treatments and their abbreviations are as follows: control (T₀), *P. polymyxa* + SMS (T₁), *P. polymyxa* + EFB (T₂), *P. polymyxa* + PL (T₃), EM + SMS (T₄), EM + EFB (T₅), EM + PL (T₆). All treatments were watered twice a day with 50 ml distilled water to maintain 60% of the maximum water holding capacity. Each inoculant of approximately 60 ml volume was poured once a month, and the control treatments were treated with 50 ml deionized water instead. Soil mixture was incubated for 90 days. After incubation,

soil samples were collected from each pot and mixed according to the treatment applied to ensure homogeneity before analysis.

Inoculants Preparation and Organic Input Material

The plant growth-promoting bacteria (PGPB), *Paenibacillus polymyxa* ATCC 825, was obtained from the American Type Culture Collection (ATCC). The PGPB strain was preserved in sterile cryovial tubes containing nutrient broth (NB) with 20% glycerol (Chemiz, Malaysia) and stored in the deep freezer at -80°C . *P. polymyxa* ATCC 825 was activated on nutrient agar (NA) to prepare the inoculant. NA was composed of (g L^{-1}) yeast extract 2.0 (HiMedia, India), peptone 5.0 (Merck, Germany), sodium chloride 5.0 (Merck, Germany), and agar 15.0 (Sigma-Aldrich, USA). The pH was adjusted to 7 before autoclave and incubated at 30°C . After 24 h of incubation, the cells on the solid medium were collected and further grown in an optimized liquid medium composed of sucrose, 30 g L^{-1} yeast extract (HiMedia, India), 30 g L^{-1} dipotassium phosphate (Merck, Germany), 5.72 g L^{-1} ammonium nitrate (Daejung, Korea), 5 g L^{-1} potassium dihydrogen phosphate (Merck, Germany), 1.9 g L^{-1} and magnesium sulfate (Merck, Germany), 0.5 g L^{-1} for 24 h at 30°C and under agitation speed 150 rpm. When the growth of *P. polymyxa* ATCC 825 reached the stationary phase after 16 h cultivation with 10^8 Colony Forming Unit (CFU) mL^{-1} , the broth was repeatedly centrifuged and suspended in 100 mM phosphate buffer.

Commercial EM-1 was activated according to the manufacturer's instructions. Activation was carried out by incubating the mixture of EM-1 and sterilized molasses with 20 parts water for 7 days, which comprised approximately 10^7 CFU ml^{-1} of fungi and 10^8 CFU mL^{-1} of bacteria. According to the standard inoculation procedure, 10 ml of activated EM-1 was diluted with 1000 ml distilled water before addition to soil amendments. This activated EM-1 solution was referred to as EM hereafter.

Different agro-waste materials, referred to as organic amendment, were obtained from the nearby fresh market and mass mushroom cultivation farm. Spent mushroom substrate (SMS) from *Pleurotus ostreatus* species was kindly obtained from C&C Mushroom Cultivation Farm, Grisek province, state of Johor, Malaysia. All organic amendments, including EFB of palm oil and pineapple leaf PL residue, were properly ground to 1–2 cm in diameter using the multipurpose grinder. These organic amendments were dried in a 60°C oven. Then, dried organic amendment materials were thoroughly mixed with sandy soil with a ratio of 2:1. The total weight for each pot treatment was approximately 3 kg.

Soil Sampling

Samples were collected 90 days after incubation. Soil samples were collected from all the pots at the soil depth of 0–15 cm depth from the surface and kept in polyethylene bags. All visible vegetation residues were removed from the soil samples. The soil samples

were divided into subsamples for physicochemical and microbial community analysis. One subsample was evenly mixed, air-dried, sieved at 2 mm-sieve, packed in zip lock plastic bags and kept at 4°C prior to commencing soil physicochemical analysis. The other subsample was stored in a -80°C freezer prior to Deoxyribonucleic Acid (DNA) extraction.

Analysis of Soil Physicochemical Properties

The soils were analyzed for pH, Electrical Conductivity (EC), soil moisture, carbon to nitrogen (C/N ratio), and nutrient contents (P: phosphorus and K: potassium). Soil pH and EC values of the soil were measured in a ratio of 1:2 (w/v) soil to water suspension using a pH meter (Mettler Toledo, Germany). 20 g of soil was weighed in a plastic bottle, and 40 ml of distilled water was added. The soil was shaken and left standing overnight for more than 16 h. The sample was shaken overnight before pH and EC values were read. The moisture content was determined by drying the soil sample with an oven (Memmert, Germany) at 105°C until it reached constant weight. About 10g of soil was weighed in a porcelain dish. The oven was heated at 105°C until the weight was constant, and the soil sample was left in the oven for two and a half hours. Then, the soil was cooled in a desiccator. Finally, the soil was weighed and recorded. The C/N ratio was mathematically calculated from organic carbon (OC) and total nitrogen (TN). Organic carbon (OC) and total nitrogen (TN) were analyzed via the Dumas method based on results obtained from the CHN analyzer (PerkinElmer, Model 2400 Series, USA). Other P and exchangeable K contents were measured using inductively coupled plasma-optical emission spectrometry (PerkinElmer, Model Optima 8300, USA).

Dry aggregate stability was determined by placing air-dried samples on a stack of sieves without breaking the soil structure. Then, 75g of soil samples were analyzed through sieving to separate the samples into different aggregate size fractions, including 4000-, 2000-, 1000-, and 250-mm mesh openings. The stack was shaken horizontally, by hand, at a rate of 30 times per minute for 2 min. The resulting aggregate fractions were gently removed from the sieves. The dry-sieving method was repeated with a second sub-sample of dried soil to determine the distribution of aggregate fractions (Castellanos-Navarrete et al., 2013). The calculation of soil aggregation is as follows:

$$W_t \text{ (g)} = (W_{t1} - W_{t2})$$

$$\text{Distribution of aggregates (\%)} = W_t/W_{t3} \times 100$$

Where, W_t = Weight of aggregates in each sieve group (g), W_{t1} = Weight of aggregates in each sieve group plus sieve can (g), W_{t2} = Weight of empty sieve can (g), W_{t3} = Total weight of soil (g).

For water holding capacity analysis, soil samples were thoroughly air-dried before analysis. After plugging one end with cotton, two long cylindrical tubes were filled with the weighed amount (100 g) of soil samples. Both the tubes were clamped in a vertical position. Then, water was slowly poured and allowed to percolate through the soil by gravitational pull. When the soil was saturated, the pouring of water stopped, and the tubes were allowed to stand until all the gravitational water had drained. The wet soil was then taken out from the tubes, and the amount of retained water was determined by weighing and drying. The amount of water retained by 100 g of original dry soil gave the field capacity of the soil, which can be calculated from the following formula according to Brischke and Wegener (2019):

$$\text{Water holding capacity (\%)} = (\text{Weight gain at saturation point/Soil dry weight}) \times 100\%$$

DNA Extraction, 16S rRNA Sequencing and Data Processing

Total DNA from 0.5 g soil samples was extracted using the soil DNA Isolation Kit method (Omega, Norcross, USA). DNA concentration was determined using a NanoDrop 2000 spectrophotometer (Thermo Scientific, Wilmington, USA) and DNA integrity was detected using 1% agarose gel electrophoresis. Polymerase Chain Reaction (PCR) amplification and high-throughput sequencing were undertaken on 16S rRNA V3-V4 region using primers 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-ACTCCTACGGGAGGCAGCA-3') (Wang et al., 2015). PCR reactions were performed in triplicate at a final volume of 20 μ l containing 4 μ l of 5 x FastPfu Buffer, 2 μ l of 2.5 mM dNTPs, 0.8 μ l of each primer (5 μ M), 0.4 μ l of FastPfu Polymerase, and 10 ng of template DNA. The PCR reaction procedure was performed as follows: 95°C for 3 min, 30 cycles, 95°C for 30 s, 55°C for 30 s, 72°C for 45 s, 72°C for 10 min. The amplification product was detected using 2% agarose gel electrophoresis. After measuring the concentration of the purified product, the equimolar number was mixed. Sequencing was performed using an Illumina MiSeq platform (Illumina, San Diego, USA) according to the standard protocol of Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). Operational taxonomy units (OTUs) were clustered at a 97% similarity cut-off using USEARCH (version 7.1). Chimeric sequences were removed. OTUs were classified with the Ribosomal Database Project (RDP) classifier (<http://rdp.cme.msu.edu/>) against the Silva 16SrRNA database using a confidence threshold of 70% (Quast et al., 2012).

Statistical Analysis

The results were initially collated with Excel 2010 (Microsoft, USA) before analyzing using Statistical Packages for Social Sciences (SPSS, USA). One-way variance (ANOVA) and Duncan's multiple comparisons were performed. Mean comparisons between treatments

were performed at a significant level of $p < 0.05$. The Pearson correlation test was performed to determine the relationship. The tables and figures were produced using ORIGIN Pro 8.0 (Origin Lab). The OTU dataset calculates Chao 1 and Shannon-Simpson's diversity indices. Results were visualized by using R 3.2.3.

RESULTS

Changes in Physicochemical Soil Properties After Microbial Inoculation and Amendment with Organic Residues

Changes in soil pH, EC, and moisture content after 90 days of incubation are illustrated in Table 2. Statistical analysis revealed that all treatments with respect to different organic amendments lead to a pH value increase. *P. polymyxa* inoculation with SMS organic amendment significantly increased to neutral pH at 7.0, higher than the previous untreated soil sample. The highest pH was found in EM+SMS (8.4), while the pH in Control+EFB was the lowest at 5.2. While pH value showed an overall increase in all soil samples, soil EC resulted in a stronger reduction, lower than the untreated sample before the experiment started. No obvious differences were observed in EC values between treatments, except 3.8 dSm^{-1} from *P. polymyxa* inoculation and PL amendment. After soil amendment, the changes in moisture content were clearly distinctive among all treatments. As shown in Table 2, higher moisture content (83.9%) was observed in soil amended with PL as organic input, which *P. polymyxa* addition to PL appeared to rank the highest. Similarly, compared to PL amendment, *P. polymyxa* inoculation with EFB amendment significantly increased moisture content very reasonably, higher than those in EFB untreated control and EM+EFB samples, respectively. Here, it is interesting to mention that the increase in moisture content due to SMS amendment, regardless of microbial inoculations, was within suitable range for soil amelioration.

Overall, the dominant size fraction was $>2 \text{ mm}$ aggregates, accounting for more than 60% of the total dry-stable aggregate (Table 2). The effect of *P. polymyxa* and EM inoculation with SMS amendment on soil aggregation was significantly higher compared to the control. The combination of *P. polymyxa* and EFB resulted in the lowest soil aggregation at 10.2%, whereas *P. polymyxa* with SMS showed much higher aggregation at 44.4%. Looking at EFB and PL as organic amendment materials, EM inoculation increased soil aggregation by 38.9% and 22.9% as compared to the untreated control, respectively. The effect of organic amendment following microbial inoculation on water-holding capacity is illustrated in Table 2. Water holding capacity significantly increased in soil inoculated with *P. polymyxa*, SMS, and EFB as an organic amendment, except for PL residues. Water holding capacity increased significantly with microbial inoculation in *P. polymyxa* and EM, regardless of organic residue variations. Our results revealed that water-holding capacity increments in response to the *P. polymyxa* inoculation; the highest was recorded at 80.2%

Table 2

Effect of organic amendments and microbial inoculation on soil physicochemical properties

Parameters	Organic residues	Microbial inoculation		
		Control	<i>P. polymyxa</i>	EM
pH	SMS	8.1 ± 0.1 ^a	7.0 ± 0.1 ^b	8.4 ± 0.1 ^a
	EFB	5.2 ± 0.1 ^a	6.3 ± 0.1 ^b	6.1 ± 0.1 ^b
	PL	6.4 ± 0.1 ^a	8.1 ± 0.1 ^b	7.9 ± 0.1 ^b
EC (dSm ⁻¹)	SMS	2.4 ± 0.2 ^a	2.6 ± 0.2 ^a	2.4 ± 0.2 ^a
	EFB	1.6 ± 0.2 ^b	1.4 ± 0.1 ^b	1.9 ± 0.1 ^b
	PL	3.5 ± 0.3 ^a	3.8 ± 0.6 ^a	3.3 ± 0.3 ^a
Moisture content (%)	SMS	40.3 ± 0.8 ^a	48.3 ± 0.1 ^a	45.3 ± 0.8 ^a
	EFB	16.1 ± 0.2 ^b	41.1 ± 0.1 ^a	12.5 ± 0.1 ^b
	PL	65.9 ± 0.8 ^a	83.9 ± 0.6 ^b	70.7 ± 0.3 ^b
P concentration (mg kg ⁻¹)	SMS	22.3 ± 0.1 ^a	60.3 ± 0.1 ^b	27.9 ± 0.1 ^b
	EFB	13.2 ± 0.1 ^a	35.1 ± 0.1 ^b	12.7 ± 0.1 ^a
	PL	30.3 ± 0.1 ^a	35.5 ± 0.1 ^a	25.2 ± 0.1 ^a
K concentration (mg kg ⁻¹)	SMS	173.3 ± 0.1 ^c	475.4 ± 0.1 ^a	233.7 ± 0.1 ^b
	EFB	165.6 ± 0.1 ^c	241.3 ± 0.01 ^b	210.3 ± 0.1 ^b
	PL	242.0 ± 0.1 ^b	279.4 ± 0.1 ^b	231.1 ± 0.1 ^b
Soil aggregation (%)	SMS	15.0 ± 0.1 ^a	44.4 ± 0.1 ^b	40.7 ± 0.1 ^b
	EFB	32.2 ± 0.1 ^a	10.2 ± 0.1 ^b	38.9 ± 0.2 ^a
	PL	15.9 ± 0.1 ^a	19.9 ± 0.1 ^a	22.9 ± 0.5 ^a
Water holding capacity (%)	SMS	37.7 ± 0.9 ^b	80.2 ± 0.1 ^a	70.2 ± 0.1 ^a
	EFB	37.6 ± 0.1 ^b	60.1 ± 0.1 ^a	30.2 ± 0.1 ^b
	PL	30.1 ± 0.1 ^b	40.2 ± 0.1 ^a	60.1 ± 0.1 ^c

Note. SMS=Spent mushroom substrate; EFB=Empty fruit bunch of palm oil; PL=Pineapple leaf residues; EM=Activated EM-1; Significant at $p<0.05$. Within each row, means with different letters are significantly different at $p<0.05$, while means with similar letters are insignificant at $p<0.05$

and 60.1%, respectively. Phosphorus (P) and potassium (K) content increased after SMS amendment and *P. polymyxa* inoculation, much higher than the initial untreated soil sample before amendment took place (Table 2). Except for K concentration, a significant difference with lower reading was detected in the soil sample amended with EFB+*P. polymyxa* and PL+*P. polymyxa* compared to previously untreated soil samples. Meanwhile, the availability of P soil treated by EM regardless of organic inputs compared with the initial available P showed a significant decrease ($p<0.05$). The P contents of soil samples fluctuated but reached the highest value at *P. polymyxa* inoculation of SMS amendment with 60.25 mg kg⁻¹. The lowest P content was recorded at EM inoculation of EFB amendment with 12.65 mg kg⁻¹. The addition of plant-growth-promoting bacteria increased the K concentration in the soil by 475.40 mg kg⁻¹, 241.28 mg kg⁻¹ and 279.40 mg kg⁻¹ in SMS, EFB and PL amendments, respectively. Compared with EFB, SMS significantly increased the availability of P in soil, while PL was slightly better than control pots in terms of P concentration.

C/N ratio values showed a significant increase in all organic amendments and microbial inoculation over 90 days' incubation compared to the initial untreated control (Figure 1). The maximum values of the C/N ratio were observed in amended soil treated with SMS along with *P. polymyxa* in comparison to other treatments. An improvement up to the recommended value in the C/N ratio was achieved by SMS amendment with both inoculations of *P. polymyxa* (15.6) and EM (18.7), respectively. However, the C/N ratio value in the EFB amendment showed a slight increase to 8.67 from the initial 6.3 in the EM inoculation, and EM+PL increased to 10.4 from the initial 8.03.

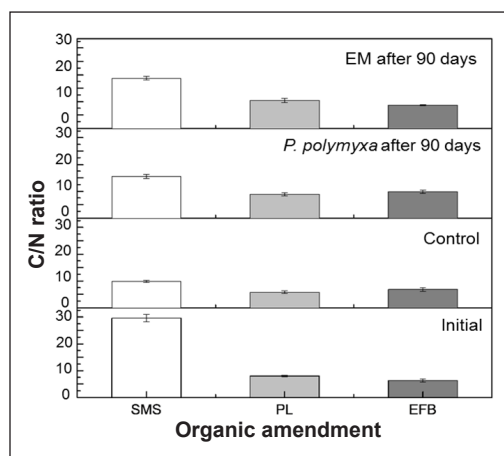


Figure 1. Changes in soil C/N ratio value under different organic amendments. SMS= spent mushroom substrate; PL=pineapple leaf residues; EFB= empty fruit bunch of palm oil before and after 90 days incubation. Error bars represent the standard deviations ($n=3$), and the bar graphs hide some error bars

Diversity and Taxonomic Composition of the Soil Bacterial Community

A total of 216,178 bacterial 16S rRNA sequences were obtained from two samples (PBS1: Initial SMS amendment and PBS2: SMS-amended soil with *P. polymyxa* after 90 days) (Table 3). Classified operational taxonomic units (OTUs) belonged to 29 phyla among all treatments based on a cut-off value of 97%. *P. polymyxa* inoculation led to significantly higher bacterial species observed and richness (Chao1) as compared to initial samples. The amendment following inoculation impacted the ACE (abundance-based coverage estimators) index significantly. However, no insignificant differences were recorded in bacterial diversity (Shannon and Simpson). These results show that organic amendment following microbial inoculation changes the diversity of the soil bacterial community. Bacterial communities in soils were dominated by phyla abundance of *Proteobacteria* (33%), *Firmicutes* (18%), *Actinobacteria* (14%), *Bacteroidata* (12%) and *Verrucomicrobia* (6%) (Figure 2a). These taxa accounted for more than 83% of the bacterial sequences in all the treatments.

The relative abundance of *Firmicutes*, *Bacteroidata* and *Verrucomicrobiota* was noticeably a bit increased by 17.4%–18.1%, 12.3%–12.4%, and 5.1%–5.8%, respectively. Other phyla (< 3% abundance, *Myxococcota* and *Chloroflexi*) accounted for 6.1% of total bacteria abundance. At the family level, the ten most abundant were *Paenibacillaceae*, *Shingomonadaceae*, *Bacillaceae*, *Cellulomonadaceae*, *Comamonadaceae*, *Rhizobiaceae*, *Brevibacillaceae*, *Chitinophagaceae* and *Streptomycetateae* (Figure 2b). The relative

Table 3

Summary of high throughput sequencing data and diversity indices

Sample name	No. of sequences	Observed species	Chao1 index	Shannon	Simpson
PBS1	104099	699 ^a	701 ^a	5.68 ^a	0.992 ^a
PBS2	112444	863 ^b	867 ^b	5.79 ^a	0.993 ^a

Note. Different letters shown after values with the same column indicate significant differences ($p < 0.05$)

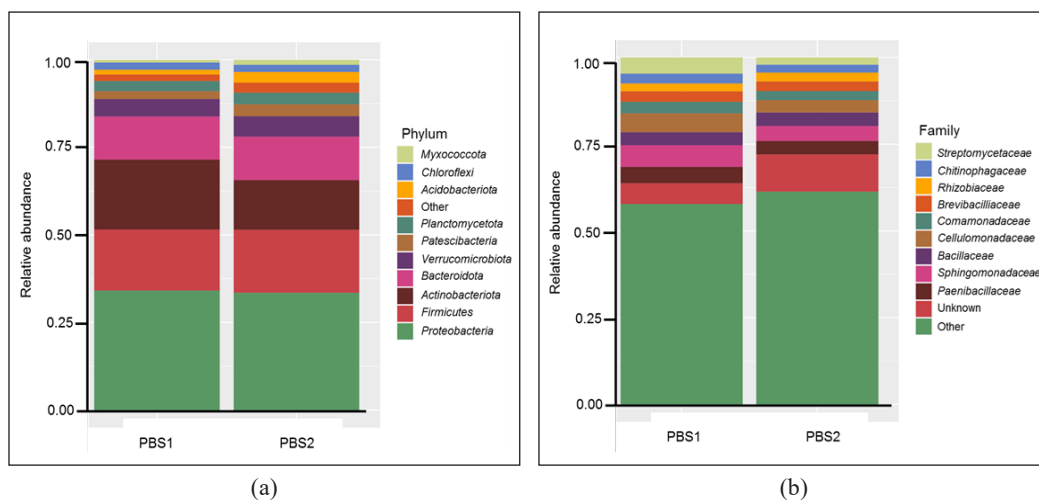


Figure 2. Relative abundance (%) of dominant bacteria taxa. Dominant bacterial phyla (a) and family (b) in both soil samples, PBS1 and PBS2, refer to different soil samples subjected to initial and final samples, respectively

abundance of unknown bacterial groups showed an increment shift by 57.7%–61.3% at the family level after 90 days' amendment. After the amendment and inoculation period, the relative abundances of *Paenibacillaceae*, *Sphingomonadaceae* and *Cellulomonadaceae* significantly decreased by 4.6%–3.9%, 6.2%–4.3%, and 5.4%–3.5%, respectively in soils compared with initial soils.

DISCUSSION

In the present study, changes in the physicochemical properties of soil were likely confirmed, and the usage of SMS, EFB, and PL could improve the pH of acidic sandy loam soil to a neutral condition suitable for any agricultural reclamation. This result was in harmony with the findings by Laurent et al. (2020), as they explained that an increased pH was attributed to a long-term application of the organic amendment. Amendment with organic-rich agro-waste was found to be successful in lowering EC values towards an acceptable limit for agriculture application. Compost with high or low EC was not recommended for crop cultivation as it could potentially cause root injury and burning, whereas low EC affects the

absorption ability of mineral elements from the soil (Manirakiza et al., 2021). Huerta-Pujol et al. (2010) reported that an optimum range of EC for field application should be between 2–4 dS m⁻¹, which was in line with our findings. EC values are expected to decrease with SMS-compost amendment, according to the recent result reported by Carpio et al. (2023). It is commonly known that the fertility of sandy loam soil could be improved by applying organic residue amendment, which was related to stable EC values.

Paula et al. (2017) showed that SMS amendment either by *P. polymyxa* or EM had increased soil moisture content within the allowable range (40%–60%). Instead of improving water-holding capacity, organic residue amendment could affect C allocation and increase soil water dynamics by 27%–37% within a short-term period (Villa et al., 2021). Managing moisture levels leads to a successful decomposition rate following microbial inoculation as it influences the process of organic matter formation. SMS amendment, together with bacterial inoculation in the present study, had a positive effect on the enhancement of the soil's ability to retain water. It indicates that moisture content may indirectly contribute to microbial proliferation, thus accelerating chemical solubility for crop uptake. Additionally, being too humid is unsuitable for decomposition, which may produce odors and potentially harmful gasses.

Our result showed that *P. polymyxa* inoculation enhanced soil aggregation by 44.4%, the highest percentage among the others. Wu et al. (2014) reported that extracellular polymeric substances (EPS) produced by *Paenibacillus* sp. have a role in speeding up sand stabilization and aggregation improvement. Potentially, EPS-producing bacteria improve soil fertility physically and biochemically and can maintain moisture availability during harsh conditions for their survival. These EPSs have been reported in previous reports (Othman et al., 2018) concerning other bacterial species. Even in our current result highlighting the optimal EPS derived from *P. polymyxa*, ATCC 824 appears as a homogenous spherical shape for aggregation improvement in root-adhering soil (Daud et al., 2023). Yet, we believe that EPSs of *P. polymyxa* are involved in ensuring the processes of biofilm flocculation prior to the appearance of other rhizosphere microbial species and adhesiveness of soil particles, as noted by Yegorenkova et al. (2013) and Grinev et al. (2020). Because sandy soil has low clay content, these soil particles could be bound by EPS-derived polysaccharides associated with glycosidic linkages.

Plant residues or any organic biomass input used as an amendment material has been shown to significantly promote the stability of soil aggregates, which bind soil particulates to form stable macro aggregates (Huang et al., 2017; Xue et al., 2022). In support of this, dried-brownish and fine-structured materials such as SMS are applied as composted amendments with the help of microbial inoculation to enhance soil carbon C sequestration. Composting carbonaceous materials could help build productive soil and lead to greater capacity for nutrient storage with subsequent accumulation of organic C (Verchot et al.,

2011). In this way, nutrient loss via leaching could be avoided, and the availability of P concentration could be recovered, as reported by our study. In comparison with EFB, SMS significantly increased soil P availability as follows: *P. polymyxa*+SMS; 60.62 mg kg⁻¹, much better than others. We hypothesized that cellulose-producing *P. polymyxa* would be a critical factor in fastening the decomposition rate for nutrient readiness. Interestingly, even though other organic residue inputs were applied simultaneously to the treated sandy soil, the K concentration in SMS amended with *P. polymyxa* was significantly higher (475.406 mg kg⁻¹) than others, suggesting that K availability was attributed to the large proportion of woody material from composted SMS (Lou et al., 2015). The resultant changes from organic residue amendment typically led to greater plant nutrient availability in the soil.

We observed that bacterial diversity indices evidently increased; the compositions of soil bacterial communities changed in PBS2 compared with those in PBS1 soil. Surprisingly, the organic amendment generated more observable species, increasing the number of species detected. In this present study, the relative abundance of potential beneficial taxa like *Proteobacteria*, *Firmicutes*, *Actinobacteriota* and *Bacteriodata* were the main dominant bacterial group after the treatment with *P. polymyxa*, suggesting that the introduction of *P. polymyxa* facilitated native soil bacteria, which is in accordance with the previous studies (Dai et al., 2017; Suleiman et al., 2019). Reduced abundance of *Actinobacteria* taxa in relation to the final amendment has been associated with the finished degradation of lignocellulose polymer materials (Lacombe-Harvey et al., 2018). In contrast, *Chloroflexi* decreased as a result of competition from similar preferred niches in the soil. Also, the lower presence of *Acidobacteriota* was likely due to stable soil pH after soil amendment, which was unfavorable for this bacterial phylum (Kielak et al., 2016). It should be noted that their abundance and activities exhibited positive correlations with some soil microorganisms following organic material addition. In response to microbial inoculation and SMS amendment, small-scale disturbances and changes in the structural soil resident bacterial community were observed. However, this phenomenon has been described as a resilient response by the soil microbial community by which they return to their original composition after being ‘disturbed’ (Lourenço et al., 2018). The relative abundance of *Paenibacillaceae*, *Shingomonadaceae*, *Bacillaceae*, *Cellulomonadaceae*, *Comamonadaceae* and *Rhizobiaceae* at the family taxonomic level is expected to result in enhanced cycling of essential nutrients, which might be crucial in improving soil fertility (Monreal et al., 2017; Schmid et al., 2017; Wang et al., 2021). Although this work provided information about how microbial inoculation and organic amendment affect the resident bacterial communities, future studies should consider comparing the seasonal microbial succession and inter-kingdom interactions in the long-term experiment. Taken together, we believe that organic amendment and PGPB promote a synergistic effect by shifting the soil microecology and ameliorating soil fertility.

CONCLUSION

The application of organic amendment, particularly SMS combined with PGPB and *P. polymyxa* inoculation, seems to be helpful in the reclamation of sandy loam soil by improving physicochemical properties and fertility (status of nutrient concentration and microbial diversity). However, adequate selection of bacterial strains must be taken into consideration when reconstructing this soil restoration technology. It can be concluded that during the decomposition of organic residues in soils, more aggregate formation led to greater persistence of nutrients in the soil and water holding capacity. The data obtained gives complementary insights into the substantial change of the soil-dominant bacterial community structure to applied amendment approaches, which can be correlated with a selection of organic material inputs and studied microorganisms. Prospective analysis should be considered, apart from studying bacterial communities, as well as other inter-kingdom partners in the soil, which are fungi, archaea and protozoa. Although a simple model of potting soil was used, it allows less complex interpretation than in open-field application. The use of carrier-based inoculant technological development should be considered for future investigations.

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