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Investigating the Potential of Endophytic Lactic Acid Bacteria Isolated from Papaya Seeds as Plant Growth Promoter and Antifungal Agent

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ABSTRACT

Endophytic lactic acid bacteria (LAB) isolated from papaya seeds, including a consortium of two LAB isolates, *Weissella cibaria* PPKSD19 and *Lactococcus lactis* subsp. *lactis* PPSSD39 could previously inhibit papaya dieback disease causative agent, *Erwinia mallotivora* BT-MARDI *in vitro*, indicating their potential as biofertilizer. However, further characterizations on other plant growth-promoting (PGP) properties of the LABs are pre-requisite to use in agricultural settings as bio-inoculum. Hence, this study aimed to evaluate PGP potentials further and *in vitro* antifungal activity of the LABs against various plant pathogens. The LAB isolates were tested positive in indole-3-acetic acid (IAA), siderophore, and ammonia production and could solubilize phosphate. *Weissella cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 exhibited the strongest *in vitro* antifungal activity against *Fusarium oxysporum* TKA and *Curvularia lunata*. Inoculum concentration of $1x10^8$ cfu/ml of

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W. cibaria PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 mixture showed the highest increment in shoot and root dry weight. In conclusion, *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 consortium displayed promising plant probiotic potential. These results highlighted the possibility of the bacterial consortium to be exploited as bioinoculant to promote plant growth and inhibit phytopathogens causing plant diseases.

Keywords: Antimicrobial activity, bioinoculant, endophytes, lactic acid bacteria, plant growth promotion

INTRODUCTION

Plant growth-promoting bacteria (PGPB) are the bacterial group that stimulates the growth of their plant host, resulting in yield improvement of crops. Their functions are highly diverse, such as nitrogen fixer (Pham et al., 2017), secondary metabolites inducer (Doumbou et al., 2001), nutrient solubilizer (Giassi et al., 2016), and also as biological control agents (Morales-cedeno et al., 2020). PGPB can supply indole-3-acetic acid (IAA) that improves the fitness of the plant root growth and plant nourishment uptake (Nimnoi & Pongslip, 2009; Passari et al., 2015). The PGPB produces several numbers of antibiotics that are good phytopathogen combatants. Certain PGPB could produce an enzyme that is essential in helping the bacteria to allocate itself into the plant tissue. Despite wealth resources on the use of rhizobacteria as a plant growth promoter, the information on lactic acid bacteria (LAB), which are commonly found in the plant endosphere, is rather limited.

LAB is a Gram-positive bacterium that yields lactic acid as one of the end products of the fermentation process. Among the plant, growth-promoting mechanisms of LAB is the production of organic acids, which result in a decrease in pH, accumulation of hydrogen peroxide, and antimicrobial secondary metabolites (Caplice & Fitzgerald, 1999). Due to their antimicrobial properties and Generally Regarded as Safe (GRAS) status, LABs are used in the food processing industry for various purposes. It suggests that the LAB is also potentially utilized in the agriculture industry as it poses no or little safety risk towards edible crops (Lutz et al., 2012), livestock, and human (Stiles & Holzapfel, 1997). LAB, such as *Lactobacillus,* has been proven to promote the growth of various plants (Shrestha et al., 2014). Plants treated with the bacteria showed higher yield, raised plant biomass and chlorophyll content, and enhanced the seedlings' growth rate (Mohite, 2013; Rzheyskaya et al., 2013; Shrestha et al., 2014; S. M. Kang et al., 2015).

Microbial inoculant is gaining more attention among farmers nowadays due to their agricultural sustainability and safety compared to chemical pesticides or fertilizers. To develop a good multi inoculant according to Bashan et al. (2014), 1) the efficiency of their resulting plant growth-promoting effects, 2) compatibility between the strains, 3) the symbiotic effect between the strains, and also 4) the potential

of biofilm formation must be explored. A microbial inoculant that can attack several pathogens simultaneously, besides promoting plant growth, might be more economical and attractive to consumers.

This study explored several LABs isolated from papaya seeds, then assessed the selected two antibacterial LABs, *L. lactis*, and *Weissella* sp., on plant growth promotion and antifungal properties. *Lactococcus lactis* is widely used in food fermentation, especially cheese and yogurt production. It has been isolated from various kinds of plants, including *Eucalyptus* (Procópio et al., 2009), sugar cane (Beneduzi et al., 2013), and pepper-rosmarin (da Silva et al., 2013). It is, however, still under-utilized in agriculture until recently. According to several previous studies, *L. lactis* displayed significant plant growth-promoting activity in greenhouse trials with cabbage and later on crops (Grönemeyer et al., 2012; Somers et al., 2007). In addition to its PGP trait, *L. lactis* showed remarkable antibacterial activity against *Listeria monocytogenes* and *Staphylococcus aureus* (Enan et al., 2013). Likewise, *W. cibaria* was one of the LABs that could show antimicrobial ability (Kamboj et al., 2015). However, information regarding its capabilities in agriculture was still limited. In our previous study, *L. lactis* and *W. cibaria* have been shown to inhibit *E. mallotivora*, the causal agent of papaya dieback disease (PDD), *in vitro* (Taha et al., 2019).

As a continuation of the study by Taha et al. (2019), this study aimed to 1) determine *in vitro* plant growth-promoting property of the endophytic LAB isolates previously isolated from papaya seeds (Taha et al., 2019), 2) assess their inhibitory activity against several fungal plant pathogens *in vitro*, and 3) examining the impact of selected life bacterial inoculum (consortium of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39) of different concentrations on promoting papaya plant growth. Twenty-three antagonistic *L. lactis* and *Weissella* sp. isolates were screened *in vitro* for their plant growth-promoting potential, i.e., phosphate solubilization, IAA formation, ammonia, siderophore, and hydrogen cyanide (HCN) production and pectinase assay. A bacterial consortium consists of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 that previously showed the best disease suppression against PDD *in planta* (Taha et al., 2019) were selected and further subjected to dual culture assay and poisoned agar test *in vitro* against common plant pathogens; i.e., *C. lunata*, *F. oxysporum* TKA, *Fusarium proliferatum* B68C, *Fusarium verticillioides* B106C, and *Fusarium verticillioides* J44C. Biofilm formation capability was also evaluated. The isolates were then tested for plant growth promotion under greenhouse conditions using three-month-old papaya seedlings as a model plant. Different concentrations of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 were applied to the papaya plantlets, and shoot length and plant biomass were measured. This study highlighted the potential application of the consortium of LAB as a plant growth promoter *in planta*.

MATERIALS AND METHODS

Bacterial Sources and Culture Maintenance

Twenty-three LAB isolates that were previously shown to inhibit *E. mallotivora* (Taha et al., 2019) were utilized in this study. The strains were isolated from papaya seed, and the species identity was determined using 16S rRNA gene sequencing by Taha et al. (2019) (Table S1). The isolates were maintained in de Man, Rogosa, and Sharpe (MRS) broth (Merck, Germany) supplemented with 20% glycerol (Merck, Germany) and stored at -20 ºC freezer (Bosch, Germany).

Plant Growth Promoting Assay *In vitro*

Phosphate Solubilisation. The antagonistic LAB isolates were grown on Pikovskaya's (PKV) agar media supplemented with 0.5% tricalcium phosphate ($Ca_3(PO_4)_2$) (Merck, Germany). Bacterial suspensions grown for 16–24 h in MRS broth were pipetted onto the PKV agar media and incubated at 30 °C for two days. Clear halo zone formation of more than 0.01 cm surrounding the colonies indicates positive phosphorus (P)-solubilization ability (Passari et al., 2015). Positive control (*Klebsiella aerogenes*) was used as a comparison.

Indole-3-acetic Acid (IAA) Evaluation. The ability of LAB to manufacture IAA was calculated according to Passari et al. (2015) and Ehmann (1977). The isolates were grown in MRS broth (Merck, Germany) at 30 °C for three days. After incubation, 1 ml of each culture was pipetted into Eppendorf tubes (Eppendorf, United Kingdom). The cultures were then centrifuged at a maximum speed of 4,293 x *g* for 5 min. A volume of 1 ml of the resulting supernatant was transferred into test tubes containing 2 ml of Salkowski's reagent before being incubated for another 25 min at 30 °C in dark conditions. The positive result of IAA production is indicated by pink color development. Positive control (*Escherichia coli*) was used as a comparison. The optical densities (OD) of isolates were measured at 530 nm wavelength using a spectrophotometer (SPECTRO 23, USA). The result was correlated with the standard curve of IAA to obtain the amount of IAA produced.

Ammonia Production. The LAB isolates were tested for ammonia production according to Cappuccino and Sherman (1996). A volume of 20 µl of LAB culture was inoculated into 10 ml of peptone water (Himedia, India). The culture was then incubated at 30 °C in an incubator shaker (Yihder Technology Co. Ltd., Taiwan) at 150 rpm for 24 h. Post-incubation, 0.5 ml of Nessler's reagent (Sigma, Germany) was pipetted into the culture. Ammonia production was observed through color changes from brown to yellow. Then, OD was taken at wavelength 570 nm, and the ammonia concentration was measured by constructing the standard curve of ammonium sulfate of known concentrations. *Klebsiella pneumonia* was used as the positive control.

Production of Siderophore. LAB siderophore development was tested using Chrome Azurol S (CAS) agar (Schwyn & Neilands, 1987). Wells of 10 mm were made on the CAS agar using a sterile cork borer. The LAB antagonists were cultured in MRS broth at 30 °C overnight. Afterward, 0.5 µl of an overnight culture of LAB isolates was pipetted into the CAS agar well. The diameter of the orange-halo zone and the size of the agar well were measured using a vernier caliper (Mitutoyo, Japan). The strength of siderophore production was determined according to the following: + represents < 5 mm wide halo zone (weak), ++ represents 5 to 10 mm wide halo zone (moderate), +++ represents > 10 mm wide halo zone (strong) (Gull & Hafeez, 2012). *Escherichia coli* was used as the positive control.

Hydrogen Cyanide (HCN) Production. The formation of HCN was assessed according to a protocol from Lorck (1948). Bennett agar was amended with 4.4 g l^{-1} glycine and inoculated with LAB isolates. A Whatman filter paper was dipped into 0.5% picric acid in 2% sodium carbonate for 1 min, and the filter paper was placed underneath the Petri dish lids. After overnight incubation at 30 °C, color changes to red on the filter paper indicate positive HCN production. *Klebsiella aerogenes* was used as the positive control for comparison.

Pectinase Assay. Screening for pectinase-producing LAB was performed using a pectin agar medium (Nawawi et al., 2017; Singh et al., 2015). Basal agar medium was used to screen pectinolytic-producing bacteria supplemented with 1% pectin from the citrus peel to prepare the pectin agar. Sodium carbonate was used to modify the pH of the media, and the media were sterilized by autoclaving. The wells on the pectin agar were made using a sterile cork borer. Then, 100 µl of LAB suspension grown in MRS broth were loaded into the wells of pectin agar medium. Plates were incubated at 30 °C for 24 h. Plates were overflowed with Gram's iodine (Kasana et al., 2008) to observe the halo zone, indicating positive pectinase production. Positive control (*Bacillus subtilis*) was used as a comparison in determining the clear zone (Ho, 2015; Singh et al., 2015).

Antifungal Activity

Dual Culture Assay. Dual culture assay was carried out following the methods by Tiru et al. (2013) with some modifications. Plate culture of fungal pathogens, *F. oxysporum* TKA, *F. proliferatum* B68C, *F. verticillioides* B106C, and *F. verticillioides* J44C were obtained from the Faculty of Science, Universiti Putra Malaysia. The pure culture of *C. lunata* was collected from the Faculty of Biotechnology and Biomolecular Sciences, Universiti Putra Malaysia. An agar disk of 5 mm diameter was cut out from a young culture of fungal pathogen and placed in the middle of potato dextrose agar (PDA) (BD Difco™, USA) agar plates. A loopful of fresh LAB isolate from the plate culture was streaked 2 cm away from the fungal disc on both sides. The paired culture was incubated

at 30 °C for 5–10 days. All pairings were carried out in triplicates. The monoculture of each fungal pathogen served as control. The diameter of fungal growth in the treatment plate was measured immediately when the mycelia of the pathogen in the control plate reached the edge of the plate. The percentage inhibition of radial growth (PIRG) was calculated by using the formula:

$$\text{PIRG (\%)} = \frac{(\text{Dc}-\text{Ds})}{\text{Dc}} \times 100\% \quad [1]$$

where Dc represents the diameter (measured in cm) of fungal growth on the control plate and Ds is the diameter (measured in cm) of fungal growth on the plate containing bacteria.

Poisoned Agar Test. A poisoned agar test was carried out following the method by Rahman et al. (2009) with some modifications. This method involved several fundamental steps: preparation of culture filtrates, preparation of poisoned agar plates, and poisoned agar test.

Preparation of Culture Filtrates. For each LAB isolate, 300 ml of potato dextrose broth (PDB) (BD Difco™, USA) was prepared in conical flasks and autoclaved for 15 min at 121 °C/1.05 kg/cm^2 pressure. A loopful of fresh LAB isolate from the plate culture was inoculated into the broth. The flasks were incubated in an incubator shaker (Yihder Technology Co. Ltd., Taiwan) for 16 to 24 h at 150 rpm at 30 °C. After the incubation period, the overnight cultures of the LAB isolates were filtered using a 0.22 µm membrane filter.

Preparation of Poisoned Agar Plates. Initially, 90%, 80%, 70%, 60%, 50%, 40%, and 20% of PDA (BD Difco™, USA) were prepared in conical flasks added with the culture filtrates. The agar was autoclaved for 15 min at 121 °C. Seven concentrations, 10%, 20%, 30%, 40%, 50%, 60%, and 80% (v/v) of the sterilized culture filtrates of LAB isolates were prepared and added into 90%, 80%, 70%, 60%, 50%, 40%, and 20% of prepared PDA (BD Difco™, USA) respectively. The molten PDA (BD Difco™, USA) containing different culture filtrates concentrations was poured into Petri plates and allowed to solidify.

Poisoned Agar Test. The plates were labelled as 10%, 20%, 30%, 40%, 50%, 60%, and 80% concentration of LAB culture filtrates. An agar disc of 5 mm diameter was cut out from the young culture of fungal pathogen and placed at the middle of the prepared poisoned agar plates. Inhibitory activity test for each concentration of the LAB culture filtrate against each fungal pathogen was conducted in triplicates. The Petri dishes were incubated for 5-10 days at 30 °C. The monoculture of each fungal pathogen served as control. The diameter of fungal growth in the treatment plate was measured immediately when the mycelia of the pathogen in the control plate reached the edge of the plate. The PIRG was calculated by using the formula:

$$\text{PIRG (\%)} = \frac{(\text{Dc}-\text{Ds})}{\text{Dc}} \times 100\% \quad [2]$$

where Dc represents the diameter of fungal growth on the control plate, and Ds

represents the diameter of fungal growth on the plate containing bacterial metabolites.

Plant Growth-Promoting Assay *In planta*

Weissella cibaria PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 were grown in MRS broth, shaking at 150 rpm at 30 °C for 16-24 h. The cells were centrifuged at 4,629 x *g* for 15 min. The cell pellets were adjusted to OD_{600}:1.0 with distilled water before final concentration adjustment to 10^2, 10^4, 10^6, and 10^8 cfu ml^{-1}. Both LAB suspensions were then mixed at a 1:1 (v/v) ratio. The diluted cultures were maintained at 4 °C. Finally, the LAB mixture was applied to the papaya plantlets under greenhouse conditions.

The *in planta* experiment was performed in a plant nursery located at Universiti Putra Malaysia (UPM) Serdang, Selangor (GPS coordinate: 3.0083354, 101.7047198). The average daily temperature was 28 °C with a relative humidity of 80% and 12 h of days, and 12 h of night every day (Time and Date, n.d.). All plantlets with height ranging from 30–70 cm were planted in small polyethylene bags filled with peat moss soil. All plants were labeled appropriately and organized in a randomized complete block design. Six treatments included TK: Treatment with chitosan; TC: Un-inoculated as control; T2: Treatment with 1:1 mixture strain at $1x10^2$ cfu ml^{-1} final concentration of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39; T4: Treatment of 1:1 mixture strain at $1x10^4$ cfu ml^{-1} final concentration of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39; T6: Treatment of 1:1 mixture strain at $1x10^6$ cfu ml^{-1} final concentration of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39; T8: Treatment of 1:1 mixture strain at $1x10^8$ cfu ml^{-1} final concentration of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39. The inoculation treatment was performed using the soil drench method of Abdel-Kader et al. (2012) and foliar spraying by Jaber and Enkerli (2017). Then, 5 ml bacterial mixture was applied using the soil drench method and another 5 ml using foliar spraying. Each treatment was carried out in 14 replicates. Plant height was recorded at 0 d, 30 d, and 45 d, while the fresh and dry weight of both shoot and root were recorded at the end of the experiment, which was at 45 d.

Quantitative Biofilm Production

This method was performed according to Christensen et al. (1995). *Weissella cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 isolates were grown in 10 ml of trypticase soy broth (TSB) (Merck, Germany) supplemented with 1% glucose (Merck, Germany) and incubated at 30 °C overnight. The overnight culture was diluted at a ratio of 1:100 (v/v), and 200 µl of the culture was dispensed into the wells of 96-well plate. The cultures were grown at 30 °C for 24 h. Post-incubation period, the culture of all the isolates in the 96-well were discarded. Then, the wells were washed up with 0.2 ml of phosphate-buffered saline (PBS) (pH 7.2) four times. Then, 2% sodium acetate (Merck, Germany) was added to fix the biofilm formed adhered to the wells

and stained by 0.1% crystal violet (Merck, Germany). Excess stain was discarded, and the wells were washed using deionized water. The 96-well plates were dried at room temperature, and the optical density of the stained bacteria biofilm was measured using a microplate auto reader (Tecan infinite F-50, Switzerland) at 570 nm. The experiment was repeated three times.

Statistical Analysis

All univariate statistical analyses were conducted using SPSS v. 22.0 (IBM SPSS Inc., USA). The normality of the data was analyzed using the Shapiro-Wilk test. In addition, data from the antifungal activity, plant growth-promoting assay *in planta*, and biofilm formation were subjected to analysis of variance (ANOVA), and pair-wise comparisons between the means of the treatments were analyzed by Tukey's test ($p < 0.05$).

RESULTS

Plant Growth Promoting Assay *In vitro*

Phosphate Solubilization and IAA Production. Table 1 shows the plant growth-promoting capabilities of the 23 isolated antagonists LAB. Among the 23 isolates, all LAB colonies displayed clear halo zones on PKV media, indicating their capabilities to solubilize phosphate. The diameter of the clear zones ranges from 2.44 ± 0.16 cm to 3.17 ± 0.08 cm. The lowest index was shown by *L. lactis* subsp. *lactis* PPKST 11 and *L. lactis* subsp. *lactis* PPKST4S and the highest was exhibited by *L. lactis* subsp. *lactis* PPSSD38.

All the isolates were also positive for IAA production, ranging between 2.029 ± 0.352 μg ml^{-1} to 15.223 ± 0.329 μg ml^{-1}. *Weissella cibaria* PPKSD9 and *L. lactis* subsp. *lactis* PPKST3 produced the highest IAA production with 15.223 μg ml^{-1} and 15.086 μg ml^{-1}, respectively.

All lactic acid bacteria isolates produced ammonia at levels ranging from 4.09 ± 0.27 mg ml^{-1} to 14.31 ± 0.72 mg ml^{-1}. *Lactococcus lactis* subsp. *lactis* PPKST37 and *L. lactis* subsp. *lactis* PPKST2 produced the highest ammonia value, while *W. confusa* PPKSD39 had the lowest value. All isolates were tested negative for HCN production as there were no color changes on filter papers.

Siderophore Production. All bacterial isolates also produced siderophore as indicated by clear orange halo zone formation around the colonies on the CAS agar media. The siderophore production index ranged from 0.296 ± 0.084 to 0.704 ± 0.084. The weakest producer was *W. cibaria* PPKSD29 (11.7 mm in diameter) and *L. lactis* subsp. *lactis* PPSST25, while the strongest producer was *L. lactis* subsp. *lactis* PPKST11 (15.3 mm in diameter).

Pectinase Enzyme Production Activity. Of the 23 isolates, 21 showed negative results for pectinase enzyme activity, whereas only two showed a halo zone after iodine application. The two isolates were *W. confusa* PPKSD39 and *L. lactis* subsp. *lactis* PPKSD8 with clear zone size 0.20 ± 0.02 cm and 0.15 ± 0.01 cm, respectively.

Table 1

Lactic acid bacteria isolates and their plant growth-promoting traits

Isolates	IAA production (μg ml^{-1})	Evaluation for IAA[*]	Siderophore production[£]	Phosphate solubilization[€]	HCN production[¶]	Ammonia production (mg ml^{-1})	Ammonia production[¥]	Pectinase assay[©]
Negative	0.385 ± 0.132[a]	NA	NA	NA	NA	0[a]	NA	NA
Positive	8.594 ± 0.255[b]	++	+++	+	+	13.45 ± 0.42[b]	+	+
PPKSD19[∂]	14.88 ± 0.387[b]	+++	+++	+	-	9.94 ± 0.20[b]	+	-
PPKSD29[∂]	8.986 ± 0.573[b]	++	+++	+	-	8.23 ± 0.13[b]	+	-
PPKSD34[∂]	6.812 ± 0.641[b]	++	+++	+	-	7.97 ± 0.34[b]	+	-
PPKSD37[∂]	11.667 ± 0.908[b]	+++	+++	+	-	7.63 ± 0.08[b]	+	-
PPKSD39[Ω]	14.742 ± 0.239[b]	+++	+++	+	-	4.09 ± 0.27[b]	+	+
PPKSD8[Δ]	14.261 ± 0.242[b]	+++	+++	+	-	9.06 ± 0.22[b]	+	+
PPKSD9[∂]	15.223 ± 0.329[b]	+++	+++	+	-	10.00 ± 0.44[b]	+	-
PPKST1[Δ]	7.595 ± 0.391[b]	++	+++	+	-	10.97 ± 1.15[b]	+	-
PPKST11[Δ]	2.174 ± 0.253[a]	+	+++	+	-	12.33 ± 0.14[b]	+	-
PPKST14[Δ]	8.406 ± 0.919[b]	++	+++	+	-	12.85 ± 0.25[b]	+	-
PPKST2[Δ]	10.378 ± 0.343[b]	+++	+++	+	-	14.05 ± 0.09[b]	+	-
PPKST3[Δ]	15.086 ± 0.801[b]	+++	+++	+	-	9.29 ± 0.32[b]	+	-
PPKST37[Δ]	13.574 ± 0.132[b]	+++	+++	+	-	14.31 ± 0.72[b]	+	-
PPKST4[Δ]	11.856 ± 0.151[b]	+++	+++	+	-	12.58 ± 0.03[b]	+	-
PPKST4B[Δ]	13.952 ± 0.132[b]	+++	+++	+	-	8.61 ± 0.28[b]	+	-

Table 1 (*Continue*)

Isolates	IAA production (µg ml^{-1})	Evaluation for IAA[*]	Siderophore production[£]	Phosphate solubilization[€]	HCN production[¶]	Ammonia production (mg ml^{-1})	Ammonia production[¥]	Pectinase assay[©]
PPKST4S[Δ]	13.093 ± 0.203[b]	+++	+++	+	-	13.20 ± 0.22[b]	+	-
PPKST5[Δ]	14.124 ± 0.373[b]	+++	+++	+	-	8.84 ± 0.28[b]	+	-
PPSSD1[∂]	4.130 ± 0.488[a]	+	+++	+	-	7.70 ±0.16[b]	+	-
PPSSD38[Δ]	6.377 ± 0.236[b]	++	+++	+	-	8.68 ± 0.47[b]	+	-
PPSSD39[Δ]	10.000 ± 0.388[b]	+++	+++	+	-	7.54 ± 0.26[b]	+	-
PPSSD7[Δ]	1.522 ± 0.434[a]	+	+++	+	-	11.12 ± 0.53[b]	+	-
PPSST25[Δ]	13.471 ± 0.376[b]	+++	+++	+	-	6.90 ± 0.41[b]	+	-
PPSST38[Δ]	2.029 ± 0.352[a]	+	+++	+	-	11.74 ± 0.99[b]	+	-

Note.

[*]For IAA production: (-): No activity (below 1 µg ml^{-1}); (+): Low activity (1.00 - 5.00 µg ml^{-1}); (++): Moderate activity (5.01-10.00 µg ml^{-1}); (+++): High activity (10.01 µg ml^{-1}and above)

[£]For siderophore production: (-): No clear zone; (+): Clear zone observed

[€]For Phosphate solubilizing index: (-): No clear zone; (+) Clear zone observed

[¶]For HCN Production: (-) No color changes; (+) Yellow color changes to orange

[¥]Ammonia production: (-) No color changes; (+) Brown color changes to yellow

[©]For siderophore production: (-): No clear zone; (+): Clear zone detected. + represents < 5 mm halo zone (weak); ++ represents 5 to 10 mm halo zone (moderate); +++ represents > 10 mm halo zone (strong). All isolates except negative control showed a diameter of orange-halo zone ranging from 11.7 to 15.3 mm

NA, no activity

[Δ]*Lactococcus lactis* subsp. *lactis*, [∂]*Weissella cibaria*, [Ω]*Weissella confusa* as determined by API® 50 CH or 16S rRNA gene sequencing (Taha et al., 2019)

For the IAA production assay, *Staphylococcus aureus* and *Escherichia coli* were used as negative and positive controls, respectively

For siderophore production assay, included *Bacillus subtilis* and *Escherichia coli* were used as negative control and positive control, respectively

For phosphate solubilization assay, *Klebsiella aerogenes* and *Proteus vulgaris* were used as positive and negative controls, respectively

Means with different letters are significantly different in comparison with negative control ($p < 0.05$) using ANOVA based on Tukey's Test

Antifungal Activity

Five plant fungal pathogens isolated from different plant hosts, viz. *C. lunata* (rice), *F. oxysporum* TKA (banana), *F. proliferatum* B68C (maize), *F. verticillioides* B106C (maize), and *F. verticillioides* J44C (maize) (Zainudin et al., 2017) were used to challenge the LAB isolates. All these fungal pathogens were the causal agents of many plant diseases worldwide. The mean radial growth of pathogens formed in the dual culture assay showed weak to moderate inhibition ability against fungal pathogens, ranging from 3.03% to 42.16% (Figure 1). The PIRG values of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39, relative to control, were recorded at 30.34% and 31.20%, against *C. lunata*, 42.16% and 38.73% against *F. oxysporum* TKA and 32.00% and 33.33% respectively against *F. vertcillioides* B106C, 3.03%, and 4.55% against *F. proliferatum* B68C, and 15.28% and 23.61% against *F. verticillioides* J44C (Figure 1). *Weissella cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 exhibited the highest antagonistic activity against *F. oxysporum* TKA at 42.16% and 38.73%. Both isolates, however, showed the least inhibitory activity against *F. proliferatum* B68C.

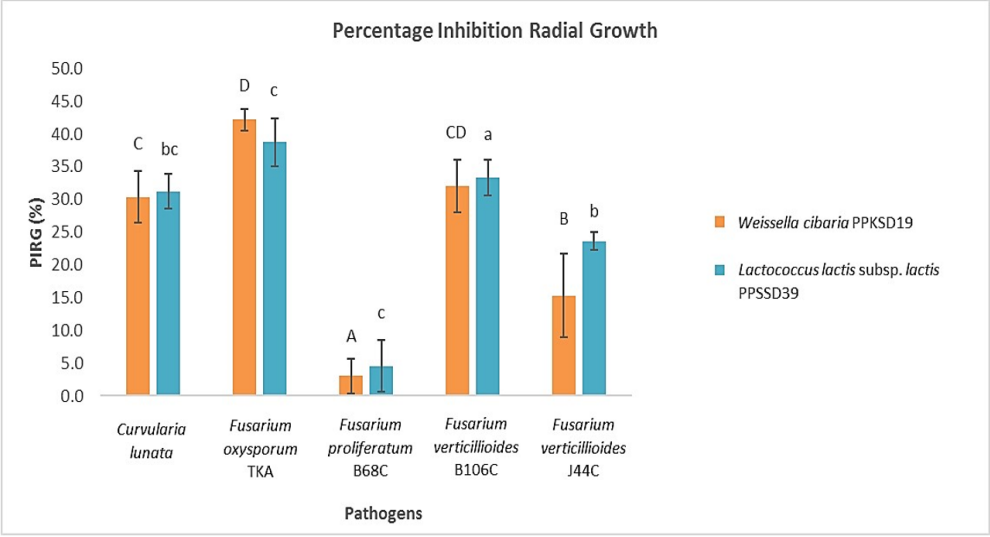
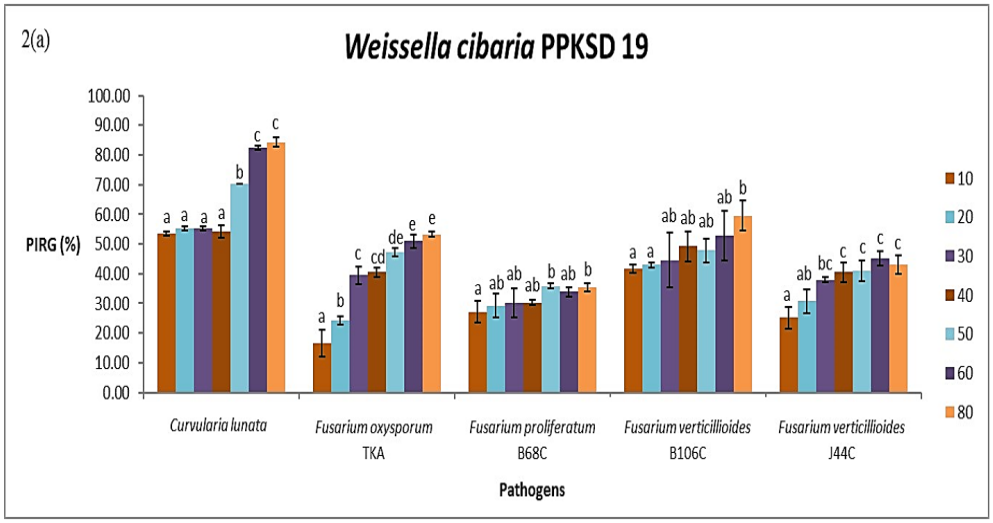


Figure 1. Percentage of inhibition of radial growth (PIRG, %) of isolates *Weissella cibaria* PPKSD19 and *Lactococcus lactis* subsp. *lactis* PPSSD39 in dual culture assay. Values are presented as means ± standard deviation (SD) of three replications. Means with different capital and small letters are significantly different ($p < 0.05$) using ANOVA based on Tukey's Test for *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39, respectively against five fungal pathogens

The antifungal activity of the LAB isolates against the representative pathogens was further confirmed with the poisoned agar test. The poisoned agar test was used to evaluate the action of secondary metabolites to control pathogen growth. The inhibition spectrum was in a dose-dependent manner as the percentage of culture filtrate containing secondary metabolites increased. The results showed weak to high inhibition against the fungal pathogens at different culture filtrate concentrations ranging from 16.67% to 84.36% (Figure 2a and Table S2). The PIRG value of *W. cibaria* PPKSD19 against *C. lunata* was comparatively higher than the other pathogens, with the lowest PIRG achieved was 53.50% at 10% of culture filtrate, and the highest PIRG was 84.36% at 80% culture filtrate (Table S2 in supplementary data). From Figure 2a, *W. cibaria* PPKSD19 had strong inhibition against *C. lunata* despite a very low percentage of culture filtrate as compared to other pathogens, which only inhibited 16.67% to 41.67% of mycelial growth at 10% of culture filtrate and 35.38% to 59.58% at 80% culture filtrate. Meanwhile, the *W. cibaria* PPKSD19 reduced the growth of *C. lunata* up to 84.36% at 80% of culture filtrate. *L. lactis* subsp. *lactis* PPSSD39 showed the highest inhibition against *F. oxysporum* TKA at 10% to 80% of culture filtrate (Figure 2b). The range of inhibition *L. lactis* subsp. *lactis* PPSSD39 against *F. oxysporum* TKA was from 43.81% to 59.05% (Table S2b and Figure S1 in supplementary data). The other pathogens, however, showed only at 22.56% to 47.33% inhibition at 10% of culture filtrate and 40.00% to 55.56% inhibition at 80% of *L. lactis* subsp. *lactis* PPSSD39 culture filtrate. It showed that *L. lactis* subsp. *lactis* PPSSD39 has high inhibitory activity against *F. oxysporum* TKA.



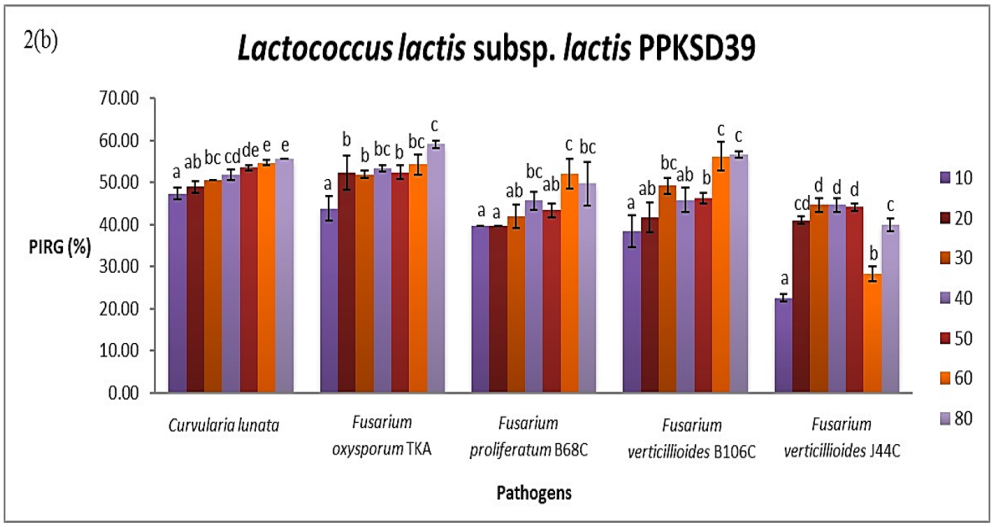


Figure 2. Percentage of inhibition of radial growth (PIRG, %) of isolates (a) *Weissella cibaria* PPKSD19 and (b) *Lactococcus lactis* subsp. *lactis* PPSSD39 in poisoned agar test. The error bars indicate standard deviations. Means with different letters are significantly different ($p < 0.05$) using ANOVA based on Tukey's test

Note. The 10, 20, 30, 40, 50, 60, and 80 indicate the percentage (%) of culture filtrate concentration (v/v)

Effect of Different Concentrations of *Weissella cibaria* PPKSD19 and *Lactococcus lactis* subsp. *lactis* PPSSD39 Mixture on the Growth Parameters of Papaya Plants

The use of chitosan as a control treatment in this study is widely used as a biofertilizer, where it could induce plant immune response towards the pathogen. Furthermore, chitosan supplementation may increase the availability of phosphate in the soil (Berger et al., 2013).

Assessment of different concentrations of the mixture of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 to promote the growth of papaya plant revealed that the growth of plantlets treated with the highest concentration of the mixture, 10^8 cfu ml^{-1}, showed a significant increment in fresh and dry weight of shoot ($p < 0.05$) as compared to the negative control (Figure 3a and Figure 3b). The dry weight of the root also increased significantly compared to negative control following treatment with 10^4, 10^6, and 10^8 cfu ml^{-1} of the LAB inoculant (Figure 3d). The fresh root also somewhat increased; however, the increment was not statistically significant ($p > 0.05$) (Figure 3c).

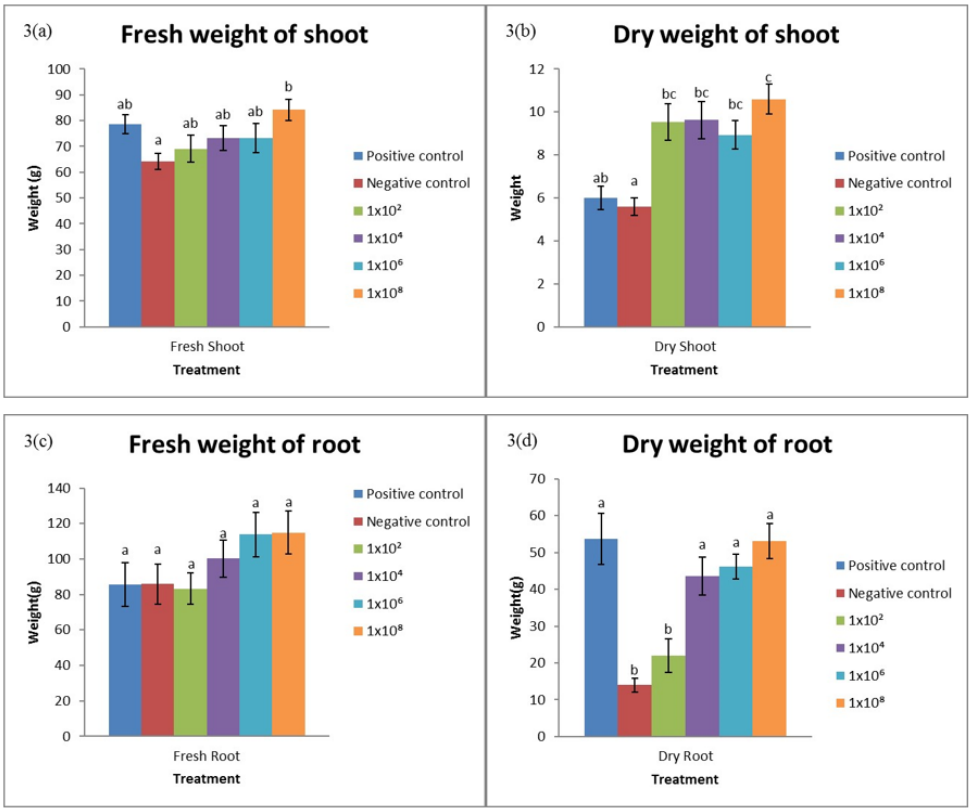


Figure 3. The effect of different concentrations of a mixture of *Weissella cibaria* PPKSD 19 and *Lactococcus lactis* subsp. *lactis* PPSSD 39 as main factors on the growth parameters of papaya plants at Day 45). (a) Fresh weight of shoot, (b) Dry weight of shoot, (c) Fresh weight of root, and (d) Dry weight of root against the different concentrations of a mixture of *W. cibaria* PPKSD 19 and *L. lactis* subsp. *lactis* PPSSD 39 treatment

Note. Each bar represents the means ± SD of 14 plant replicates. Means with different letters are significantly different ($p < 0.05$) using Kruskal Wallis (a, b, d) and ANOVA (c) based on Tukey's Test.

Biofilm Production

Quantitative biofilm production of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 isolates were determined using the microplate auto reader. There were light blue color changes in the microplate for both isolates. The low average OD_{570} nm measurement of both *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 compared to the positive control, indicating weak biofilm producers (Table 2).

Table 2

Evaluation of biofilm production by the LAB isolates

Isolates	Biofilm production (OD)*	Evaluation
Weissella cibaria PPKSD19	0.0783 ± 0.02^{a}	Weak
Lactococcus lactis subsp. *lactis* PPSSD39	0.0687 ± 0.03^{a}	Weak
¶*Listeria monocytogene*	0.2858 ± 0.05^{b}	Strong
¥Bacillus amyloliquefaciens	0.0602 ± 0.02^{a}	Weak

Note. Interpretation of biofilm production. Measurement was taken at OD_{570} nm for biofilm production
Optical density cut-off value (OD c) = Average OD of negative control + 3× standard deviation (SD) of negative control
≤ OD c / OD c < ~ ≤ 2x OD c = None/weak
2x OD c < ~ ≤ 4x OD c = Moderate
> 4x OD c = Strong
*Values are presented as means ± SD of three replications. Means with different superscript letters are significantly different ($p < 0.05$) using ANOVA based on Tukey's Test
¶Positive control strain (Strong)
¥Negative control (None/Weak)

DISCUSSION

The purpose of this study was to evaluate the plant growth-promoting ability *in vitro* and *in planta* of the 23 LAB isolates previously isolated from papaya seeds. In addition, IAA, HCN, siderophore and ammonia production, phosphate solubilization, and pectinase assay were carried out for the 23 bacterial isolates.

All of the endophytic LAB isolates could produce IAA, in which *W. cibaria* PPKSD9 and *L. lactis* subsp. *lactis* PPKSD3 showed the highest IAA production. Strafella et al. (2021) reported several *L. lactis* strains could produce a higher amount of IAA compared to the other LAB tested. Nimnoi and Pongslip (2009) reported that the IAA hormone affected plant cell elongation, and IAA-producing bacteria improved the root and shoot growth of *Raphanus sativus* and *Brassica oleracea*. Similarly, the IAA-producing *W. cibaria* and *L. lactis* used in this study have also enhanced the growth of papaya seedlings.

The highest phosphate solubilizing index was produced by *L. lactis* subsp. *lactis* PPSSD38. In a similar experiment conducted by Strafella et al. (2021), all tested *L. lactis* isolates could solubilize phosphate. Manufacturing of low molecular weight organic (Collavino et al., 2010), phytase, and alkaline phosphatase (de Lacerda et al., 2016) were proposed to mediate this property. Viruel et al. (2014) reported positive enhancement of maize plants after being treated with phosphate solubilizing bacteria. Phosphorous is one of the nutrients needed for plant growth (Khan et al., 2014). The availability of phosphorous, however, can be the limiting factor in a certain condition, thus affecting the growth of the plant significantly (Wang et al., 2010).

Hence, the phosphate-solubilizing LAB may help provide the plant with nutrients needed and increase growth.

All the tested LAB isolates were positive for ammonia production, with the highest production being *Lactococcus* sp. PPKST37 and *Lactococcus* sp. PPKST2. Ammonia production is valued as root and shoot elongation assistance, resulting in higher plant biomass. According to Marques et al. (2010), opportunistic phytopathogen can also be inhibited by the overproduction of ammonia. Earlier studies mentioned that HCN is commonly involved in disease suppression in plants (Wei et al., 1991). However, a study revealed that HCN was not involved in biocontrol against pathogens but rather regulated phosphate availability (Rijavec & Lapanje, 2016). According to Rijavec and Lapanje (2016), cyanide in the HCN can improve the mineral transportability and discharge of phosphate, resulting in phosphate availability. The LAB isolates used in this study, however, did not produce HCN.

Another plant growth-promoting feature tested was siderophore production. Through the iron-binding capabilities, bacteria that produce siderophores will have the upper hand in competing with the phytopathogens, making iron unavailable for them (Bashan et al., 1980; Siddiqui, 2005). All the endophytic LAB isolates were positive for siderophore production, with the largest halo zone created by *L. lactis* subsp. *lactis* PPKST11. Marag and Suman (2018) also found that one of their endophytic *Zea mays* L. isolates could produce siderophore and later identified as *L. lactis*. In the study of unique genomic cluster matching of two *L. lactis* strain, there were clusters of unique genes of *L. lactis,* similar to the siderophore production pathway of *B. subtilis* (Siezen et al., 2008), supporting the capabilities of the *L. lactis* to produce siderophore.

Pectinase enzyme production assay recorded only two positive results, *W. confusa* PPKSD39 and *L. lactis* subsp. *lactis* 1 PPKSD8. Assamoi et al. (2016) reported that *Weissella* isolates of Wc 115 displayed pectinase activity needed for cassava dough softening. The presence of pectinase helps the bacteria to break into the plant endosphere. As hydrolase, pectinase will break down the pectin of the plant structure to help the endophytic bacteria to get inside of the plant ecosystem (Hayat et al., 2010). Since *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 lack of pectinase production, slight wound, or pre-emptive seed colonization was made to allow the *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 to infiltrate into the plant endosphere. However, this does not rule out the possibility that *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 may utilize other ways to assist them in entering the plant endosphere.

All pathogens used in the antifungal assay were the severe causal agents of plant diseases of many important plantations worldwide. *Curvularia* sp. and *Fusarium* sp. previously showed capabilities in infecting papaya plants, causing various diseases. *Fusarium semifectum* and *F. oxysporum* in the papaya plant caused fruit

rot (Zakaria et al., 2012). The wilt-inducing strains of *F. oxysporum* were responsible for severe damage on many economically important plant species (Agbaglo et al., 2020; Fravel & Larkin, 2002), commonly banana plants. Meanwhile, *F. proliferatum* is always associated with *F. verticillioides* as they cause similar plant diseases. Bullerman and Tsai (1994) reported that soil-borne *F. proliferatum*, a closely related fungus to *Fusarium moniliforme* (syn. *F. verticillioides*), is found in all corn-growing regions. On the other hand, *C. lunata* was firstly discovered from an infected papaya plant causing post-harvest disease in the fruit (Helal et al., 2018). The pathogens can also infect many other plant species, such as rice, maize, and banana (Liu et al., 2011; Tann & Soytong, 2017). This fungus secreted mycotoxin, which is responsible for plant disease. The ability of our isolates to inhibit these globally recognized pathogens highlights their potential as universal biocontrol agents for various plant diseases.

By supporting our findings, *W. cibaria* and *L. lactis* from various sources were also shown to have inhibitory activity against various fungal pathogens in food, plants, and human. *Weissella cibaria* isolated from a semolina ecosystem completely inhibited all the tested fungal species that generally contaminated the bakery product, viz. *Aspergillus niger*, *Penicillium roqueforti*, and *Endomyces fibuliger* (Valerio et al., 2009) also agree with Ndagano et al. (2011), who found that *W. cibaria* FMF4B16 isolated from mill flour and fermented cassava showed antifungal activity against food molds. A study by Trias et al. (2008) reported that *W. cibaria* strain TM128 reduced the fungal rot diameter of the Golden Delicious apple by 50%. Kim (2005) reported that *L. lactis* subsp. *lactis* isolated from Kimchi had strong antagonistic activity against *Aspergillus fumigatus*, an opportunistic pathogen causing several human diseases. It has also been reported that *W. cibaria* can inhibit *F. oxysporum* (Valencia-Hernández et al., 2016), responsible for many plant diseases. Mauch et al. (2010) also reported that *W. cibaria* has fungistatic activity against *Fusarium* species. Interestingly, there were no past reports regarding antifungal activity of *W. cibaria* and *L. lactis* against *C. lunata*, *F. verticillioides*, and *F. proliferatum*. Overall, the antagonistic activities of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 against these pathogens suggests their biocontrol potential in suppressing a wider range of plant diseases. Further experiments need to be conducted to confirm this.

The potential of the *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 consortium that previously showed outstanding ability in suppressing papaya dieback disease *in planta* (Taha et al., 2019), while displaying positive *in vitro* PGP traits in this study were further tested for their ability in promoting papaya plant growth in the absence of the pathogen. Different doses of the consortium were applied to see at which concentration it can sufficiently enhance the papaya plant growth. Interestingly, the effects of the

LAB isolates on all growth parameters were also concentration-dependent (Figure 3), suggesting a positive growth enhancement effect on the papaya plantlets. It means that the higher the concentration of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39, the higher the increment of the papaya plant shoot growth, by which a significant improvement was seen between untreated and 10^8 cfu ml^{-1} of the consortium ($p < 0.05$). The effect was comparable to that of the positive control, chitosan, suggesting they are equally competent to promote plant growth. Evaluation for the plant height assessment revealed no significant difference between the treatments.

Meanwhile, the significantly higher dry weight for aerial and underground parts of papaya plants showed the effectiveness of the bacterial mixture treatment compared to the untreated plants (Figure 3b and Figure 3d). Many researchers recorded a similar increasing pattern in plant weight inoculated with PGP bacteria (Gholami et al., 2009; Passari et al., 2015; Shrestha et al., 2014). The positive effects of *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 consortium to the papaya plantlets may be explained by their ability to produce IAA, ammonia, siderophore, and also solubilize phosphate.

Biofilm production assay showed no biofilm produced by *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39. The inability of our *L. lactis* subsp. *lactis* PPSSD39 to form biofilm was contradictory with a previous report, which stated that *Lactococcus* could produce biofilm (Zaidi et al., 2011). In a different study related to *W. cibaria*, the bacterium was discovered to inhibit the biofilm of *Streptococcus mutans* due to the production of water-soluble polymers from sucrose (M. S. Kang et al., 2006). Since *W. cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 were mixed, *W. cibaria* PPKSD19 was likely to inhibit the biofilm production of *L. lactis* subsp. *lactis* PPSSD39, resulting in lower cell distribution. It remains to be elucidated in future work.

This study showed that all isolated LAB has great potential as a plant growth promoter, as all the isolates exhibited positive results in the IAA production, inorganic phosphorous solubilization, siderophores, and ammonia production tests, and two of them in the pectinase assay. *Weissella cibaria* PPKSD19 *and L. lactis* subsp. *lactis* PPSSD39 could inhibit fungal pathogens, viz. *C. lunata*, *F. oxysporum* TKA, *F. proliferatum* B68C, *F. verticillioides* B106C, and *F. verticillioides* J44C isolated from various plant hosts, suggesting their potential in controlling other plant diseases. *Weissella cibaria* PPKSD19 and *L. lactis* subsp. *lactis* PPSSD39 inhibited *F. oxysporum* TKA and *C. lunata* the most. The greenhouse experiment showed that $1x10^8$ cfu ml^{-1} was the optimum concentration to enhance papaya plant growth significantly. These results highlighted the potential of both isolates as plant probiotics. However, further investigations must be performed to explore their potential to control various plant diseases while simultaneously increasing plant growth.

CONCLUSION

Weissella cibaria PPKSD19 and *Lactococcus lactis* subsp. *lactis* PPSSD39 consortium displayed promising plant probiotic potential by showing positive inhibition against multiple plant pathogens *in vitro*, as well as increasing fresh weight of shoot and dry weight of shoot and root of papaya plantlets. These results highlighted the possibility of the bacterial consortium being exploited as a versatile bioinoculant to promote plant growth and simultaneously suppress phytopathogens causing plant diseases. For future work, the antifungal activity of the consortium should be verified *in planta*. Furthermore, the storage stability of the consortium as bioinoculant should be optimized for longer shelf-life before commercialization and large-scale field application could be realized towards sustainable agriculture.

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SUPPLEMENTARY DATA

Table S1

List of bacterial isolates used and its sources. Bacteria was isolated from papaya seed and sarcotesta (Taha et al., 2019)

Plant tissue source	Strain	Lactic acid bacteria
Seed	PPKSD8	*Lactococcus lactis* subsp. *lactis*
	PPKSD9	*Weissella cibaria*
	PPKSD19	*Weissella cibaria*
	PPKSD29	*Weissella cibaria*
	PPKSD34	*Weissella cibaria*
	PPKSD37	*Weissella cibaria*
	PPKSD39	*Weissella confusa*
	PPSSD1	*Weissella cibaria*
	PPSSD7	*Lactococcus lactis* subsp. *lactis*
	PPSSD38	*Lactococcus lactis* subsp. *lactis*
	PPSSD39	*Lactococcus lactis* subsp. *lactis*
Sarcotesta	PPKST1	*Lactococcus lactis* subsp. *lactis*
	PPKST2	*Lactococcus lactis* subsp. *lactis*
	PPKST3	*Lactococcus lactis* subsp. *lactis*
	PPKST4	*Lactococcus lactis* subsp. *lactis*
	PPKST4S	*Lactococcus lactis* subsp. *lactis*
	PPKST4B	*Lactococcus lactis* subsp. *lactis*
	PPKST5	*Lactococcus lactis* subsp. *lactis*
	PPKST11	*Lactococcus lactis* subsp. *lactis*
	PPKST14	*Lactococcus lactis* subsp. *lactis*
	PPSST25	*Lactococcus lactis* subsp. *lactis*
	PPSST38	*Lactococcus lactis* subsp. *lactis*

Table S2

Percentage of inhibition of radial growth (PIRG, %) of isolates (a) Weissella cibaria *PPKSD 19 and (b)* Lactococcus lactis *subsp.* lactis *PPSSD 39 in poisoned agar test*

(a) *Weissella cibaria* PPKSD19

PIRG (%)	*Curvularia lunata*	*Fusarium oxysporum* TKA	*Fusarium proliferatum* B68C	*Fusarium verticillioides* B106C	*Fusarium verticillioides* J44C
10	53.50 ± 0.71^{a}	16.67 ± 4.59^{a}	27.18 ± 3.55^{a}	41.67 ± 1.44^{a}	25.13 ± 3.55^{a}
20	55.14 ± 0.71^{a}	24.29 ± 1.43^{b}	29.23 ± 4.07^{ab}	42.92 ± 0.72^{a}	30.77 ± 4.07^{ab}
30	55.14 ± 0.71^{a}	39.52 ± 2.97^{c}	30.26 ± 4.95^{ab}	44.58 ± 9.21^{ab}	37.95 ± 0.89^{bc}
40	54.32 ± 2.14^{a}	40.48 ± 1.65^{cd}	30.26 ± 0.89^{ab}	49.17 ± 5.20^{ab}	40.51 ± 3.20^{c}
50	70.37 ± 0.00^{b}	47.14 ± 1.43^{de}	35.90 ± 0.89^{b}	47.92 ± 4.02^{ab}	41.03 ± 3.55^{c}
60	82.30 ± 0.71^{c}	50.95 ± 2.18^{e}	33.85 ± 1.54^{ab}	52.92 ± 8.32^{ab}	45.13 ± 2.35^{c}
80	84.36 ± 1.43^{c}	53.33 ± 0.82^{e}	35.38 ± 1.54^{b}	59.58 ± 5.05^{b}	43.08 ± 3.08^{c}

Means with different superscript letters within rows indicate significant difference at $p < 0.05$ using one-way ANOVA

(b) *Lactococcus lactis* subsp. *lactis* PPSSD39

PIRG (%)	*Curvularia lunata*	*Fusarium oxysporum* TKA	*Fusarium proliferatum* B68C	*Fusarium verticillioides* B106C	*Fusarium verticillioides* J44C
10	47.33 ± 1.43^{a}	43.81 ± 2.97^{a}	39.73 ± 0.00^{a}	38.33 ± 3.82^{a}	22.56 ± 0.89^{a}
20	48.97 ± 1.43^{ab}	52.38 ± 4.12^{b}	39.73 ± 0.00^{a}	41.67 ± 3.61^{a}	41.03 ± 0.89^{ab}
30	50.62 ± 0.00^{bc}	51.90 ± 0.82^{b}	42.01 ± 2.85^{ab}	49.17 ± 1.91^{ab}	44.62 ± 1.54^{bc}
40	51.85 ± 1.23^{cd}	53.33 ± 0.82^{bc}	45.66 ± 2.09^{bc}	45.83 ± 2.89^{ab}	44.62 ± 1.54^{c}
50	53.50 ± 0.71^{de}	52.38 ± 1.65^{b}	43.38 ± 1.58^{ab}	46.25 ± 1.25^{ab}	44.10 ± 0.89^{c}
60	54.73 ± 0.71^{e}	54.29 ± 2.47^{bc}	52.05 ± 3.62^{c}	56.25 ± 3.31^{ab}	28.21 ± 1.78^{c}
80	55.56 ± 0.00^{e}	59.05 ± 0.82^{c}	49.77 ± 5.19^{bc}	56.67 ± 0.72^{b}	40.00 ± 1.54^{c}

Means with different superscript letters within rows indicate significant difference at $p < 0.05$ using one-way ANOVA

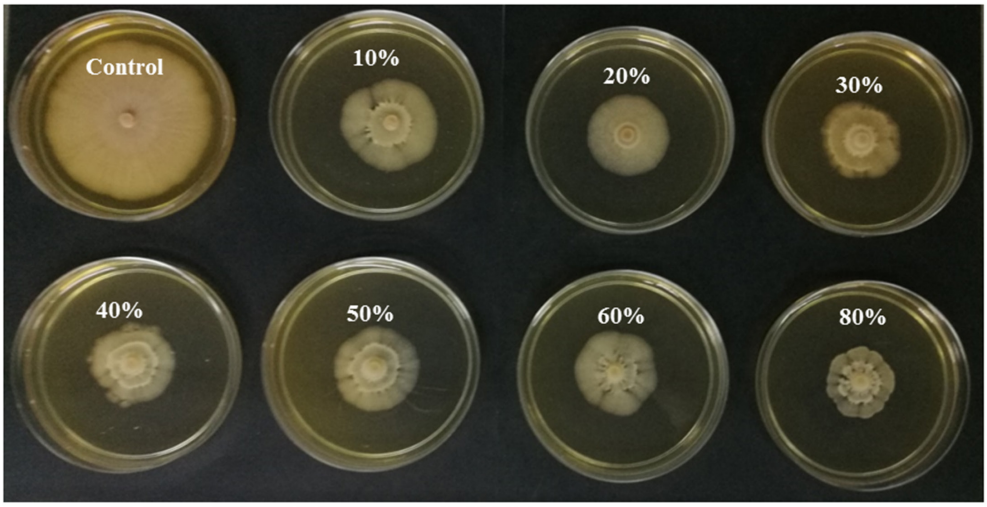

Figure S1. Antagonistic activity of different culture filtrate concentrations of *Lactococcus lactis* subsp. *lactis* PPSSD39 against *Fusarium oxysporum* TKA grown on PDA media. The PDA was incorporated with 10%, 20%, 30%, 40%, 50%, 60%, and 80% (v/v) culture filtrate concentration of 7-day old *L. lactis* subsp. *lactis* PPSSD39 cultures