



## Preserving snake fruit (*Salacca zalacca* Voss) quality: Effective control of *Peniophora salacca* SKRU002 with fungicides and biological agents

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### ABSTRACT

*Peniophora salacca* (Russulales, Basidiomycota), a newly identified pathogen of *Salacca zalacca*, is a major cause of snake fruit rot, resulting in significant agricultural losses. This study evaluates the efficacy of chemical fungicides and biological controls against *P. salacca* SKRU002, focusing on disease suppression and fruit quality preservation. Commercial fungicides (propiconazole®, prochloraz®, metalaxyl®, azoxystrobin®, thiram®) and *Streptomyces philanthi* strains RM-1-138 and RL-1-178 were tested. *In vitro*, prochloraz® (1000 µL mL<sup>-1</sup>) fully inhibited *P. salacca* growth, outperforming other fungicides. Both *S. philanthi* strains exhibited strong antifungal activity through volatile and non-volatile compounds. Additionally, autoclaved (at 121 °C for 15 min) and diluted (1/1000) bacterial culture filtrates (BCF) from both strains achieved over 55 % inhibition of *P. salacca*. In liquid culture, RM-1-138 (86.80 %) and RL-1-178 (80.86 %) demonstrated greater inhibition than metalaxyl® (9.34 %) and azoxystrobin® (56.84 %), though prochloraz® and propiconazole® remained the most effective (100 %). *In vivo*, untreated fruits inoculated with *P. salacca* showed 100 % disease incidence, significant weight loss (13.28 %), color changes ( $L^*$ ,  $a^*$ , and  $b^*$ ), and reductions in total soluble solids, total phenolic content, and antioxidant activity, while titratable acidity remained unchanged. Both biological and chemical treatments effectively controlled the pathogen and preserved fruit quality. These findings highlight the potential of *S. philanthi* strains and fungicides in managing *P. salacca*, offering promising strategies for snake fruit cultivation.

### 1. Introduction

Snake fruit [*Salacca zalacca* (Gaerth.) Voss] is a tropical fruit widely distributed across Asia, including Thailand, Indonesia, Malaysia, Cambodia, southern Myanmar, Vietnam, the Philippines, and China [1, 2]. Known for its sweet, slightly acidic, and astringent flavor, snake fruit is rich in vitamins, minerals, fiber, and bioactive compounds, contributing to its antioxidant properties [3,4]. As snake fruit gains economic importance in Thailand and neighboring Southeast Asian countries, its exports to global markets such as Russia, the United Arab Emirates, and the Maldives have increased [5].

In the cultivation, pre-and post-harvest stages of snake fruit, fungal infection presents a significant hurdle to consumer acceptance. To address this challenge and preserve the fruit's characteristic redness,

alternative methods for controlling mold growth are imperative [6]. The identification of contaminating molds plays a pivotal role in preventing and mitigating fungal contamination, particularly in snake fruit destined for export. Two species, *Marasmius palmivorus* and *Thieviolopsis* sp., have been identified as the most impactful contributors to fruit infection. *Thieviolopsis*, typically prevalent in mature fruits, triggers discoloration from brown to black, resulting in rot with mycelia visible in the affected areas, particularly pronounced during Thailand's rainy season [5]. Both *M. palmivorus* and *Thieviolopsis* sp. are associated with typical symptoms of snake fruit peeling, where the presence of mycelium in the fruit results in excessively dry fruit skin [7]. Furthermore, Boukaew et al. (2024) [8] recently identified a new species called *Peniophora salacca* (Russulales, Basidiomycota), causing rotten snake fruit. The species has been observed infecting snake fruit in Phatthalung province, resulting in

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approximately 30 % of economic losses. Therefore, the implementation of effective disease control measures for snake fruit is paramount to minimize economic losses.

The postharvest preservation of snake fruit using edible coatings is important. Once the skin is peeled, snake fruit becomes highly susceptible to microbial attack, leading to a shorter shelf life. To address these issues, the application of edible coatings can be an effective strategy to protect snake fruit from microbial penetration and thereby extend its shelf life [9]. Edible coatings, such as chitosan and essential oils, have gained attention for their ability to prolong the freshness of various fruits by creating a protective barrier that reduces moisture loss, inhibits microbial growth, and maintains fruit quality [9,10]. Given that snake fruit is highly perishable and prone to rapid deterioration, applying edible coatings could significantly reduce postharvest losses [9,10]. These coatings are typically made from natural, biodegradable materials, making them an eco-friendly option for fruit preservation.

Fungicide treatments are crucial for effectively controlling various fruit diseases. This study investigates five commonly used fungicides in Thailand: propiconazole®, prochloraz®, metalaxyl®, azoxystrobin®, and thiram®. These fungicides play a pivotal role in the management and prevention of fruit diseases. For example, prochloraz® has been used to manage postharvest fruit rot in avocados caused by *Phomopsis* sp. [11], and to combat postharvest spoilage of kinnow fruits induced by *Fusarium solani* [12]. The efficacy of propiconazole® in controlling *Phomopsis vexans* has also been demonstrated [13], while azoxystrobin® has proven effective against *P. amygdali* in peach fruit [14] and *P. vexans* in eggplant fruit [15,16]. Metalaxyl® has been shown to effectively manage leaf disease caused by *Phytophthora palmivora* in durian [17]. However, thiram® is no longer permitted for use in the EU, and existing maximum residue levels (MRLs) are being withdrawn. The EFSA (2021) evaluated import tolerances, but due to insufficient toxicological data on its metabolite M1, a consumer risk assessment could not be completed, and risks to consumers could not be excluded [18]. In this study, we used thiram® for comparison with biological control agents in disease management, though its actual use requires careful consideration.

In addition to chemical control, the utilization of antagonistic microorganisms for managing plant pathogenic fungi has been a subject of study. The absence of an effective method to control diseases in snake fruits underscores the urgent need for adopting environmentally friendly farming systems. Given this context, the investigation of biological alternatives, particularly those involving beneficial microorganisms, emerges as a highly promising approach. This strategy aims at the integrated management of plant pathogens and diseases [19,20]. A wide range of microorganisms, including bacteria such as *Bacillus* [21–23], *Pseudomonas* [24,25], and *Streptomyces* [26–29], as well as several species of *Trichoderma* [30–36], have been reported for successfully managing various plant diseases in agricultural settings.

Among these microorganisms, *Streptomyces* stands out as a promising biocontrol agent that has undergone extensive evaluation and global implementation, earning recognition for its effectiveness [26,28,29]. *Streptomyces* species are considered biocontrol agents due to their production of various active compounds, including antibiotics, enzyme inhibitors, and volatile compounds, making them valuable for agricultural applications. Moreover, they can survive in harsh environments and colonize plant roots [37]. *Streptomyces* employs multiple strategies to suppress fungal pathogens, including nutrient competition, cell wall degradation, degradation of virulence factors, and the induction of plant immunity [38].

Several species of *Streptomyces* have been isolated and utilized to control plant pathogens in various crops. Examples include managing root rot disease caused by *Phaseolus vulgaris* in beans [20], controlling root rot caused by *F. oxysporum* in *Salvia miltiorrhiza* seedlings [26], suppressing Fusarium-wilt disease caused by *F. solani* in green gram seedlings [29], addressing clubroot disease caused by *Plasmodiophora brassicae* in oilseed rape [39], and combating Fusarium-wilt disease in tomatoes and bananas caused by *F. oxysporum* [40]. Notably, strains

RM-1-138 and RL-1-178 of *S. philanthi*, isolated from the rhizosphere of chili peppers in southern Thailand [41], have exhibited broad-spectrum antagonistic activity against pathogens such as *Sclerotium rolfsii*, *Ralstonia solanacearum* [41], *Rhizoctonia solani* [42–45], *Botrytis cinerea* [46, 47], *Aspergillus parasiticus*, *A. flavus* [48–53], *Colletotrichum gloeosporioides* [54], *Penicillium digitatum* [55], and *Curvularia oryzae* [56].

The current knowledge regarding biological control using antagonistic microorganisms to manage fungal pathogens on snake fruit is limited in the existing literature. This paper aims to bridge this gap by presenting updated information on the efficacy of both strains of *S. philanthi* in controlling fungal pathogens, both *in vitro* and on snake fruit. The objectives of the present study include: (i) evaluating the potential effectiveness of biological control using both strains of *S. philanthi* and chemical control using prochloraz®, metalaxyl®, azoxystrobin®, propiconazole®, and thiram® in controlling rotten snake fruit caused by *P. salaccae* SKRU002; and (ii) determining the preservation of snake fruit quality during storage.

## 2. Materials and methods

### 2.1. Sources of materials

#### 2.1.1. Microorganisms

The antagonistic strains RM-1-138 and RL-1-178 of *Streptomyces philanthi* were previously isolated and characterized as described by Boukaew et al. (2011) [41]. These strains were subsequently cultured in glucose yeast-malt (GYM) medium, containing 0.4 % glucose, 0.4 % yeast extract, and 1.0 % malt extract, at 30 °C for 7 days. A bacterial culture filtrates (BCF) of *S. philanthi* RM-1-138 was prepared by submerged cultivation at 30 °C on a rotary shaker (150 rpm) in a 250 mL flask containing 100 mL GYM medium, with the pH adjusted to 7.0 using 5 M NaOH before autoclaving. After 3 days of cultivation, a 5 mL aliquot of the seed culture was transferred into 100 mL of fresh medium and incubated for 10 days under the same conditions. The culture broth was then centrifuged at 8880×g for 20 min and filtered through a 0.22 µm Millipore membrane [44]. The bacterial culture filtrates were designated as BCF RM-1-138 and RL-1-178.

The pathogen *P. salaccae* SKRU002 was isolated from rotten snake fruit [8]. Subsequently, the strain SKRU002 was cultured and maintained on potato dextrose agar (PDA) plates at 30 °C for seven days.

#### 2.1.2. Commercial chemical fungicides

The five chemical fungicides—prochloraz® (45 % w/v), metalaxyl® (25 % w/v), azoxystrobin® (25 % w/v), propiconazole® (25 % w/v), and thiram® (80 % w/w)—were prepared according to the respective company recommendations. Prochloraz® was prepared by adding 30 mL to 20 L of sterile distilled water, resulting in a final concentration of 0.000675 g mL<sup>-1</sup> (675 ppm). Propiconazole® and azoxystrobin® were each prepared by adding 20 mL to 20 L of sterile distilled water, with a final concentration of 0.00025 g mL<sup>-1</sup> (250 ppm). Thiram® was prepared by adding 20 g to 20 L of sterile distilled water, resulting in a final concentration of 0.0008 g mL<sup>-1</sup> (800 ppm). Metalaxyl® was prepared by adding 40 g to 20 L of sterile distilled water, with a final concentration of 0.0005 g mL<sup>-1</sup> (500 ppm).

#### 2.1.3. Snake fruit preparation

The snake fruit cv. "Sumalee" was harvested from a farm located in Thung Naree Subdistrict, Phatthalung District, Phatthalung Province, southern Thailand. With an average of 20 fruits per kilogram, the harvest took place 38 weeks after pollination. The fruits were carefully sorted based on their size and ensured to be free from any signs of disease or visible wounds. Subsequently, each fruit underwent thorough scrubbing with a brush, rinsing with sterile distilled water, and air-drying for 30 min in a laminar flow cabinet before immediate use in experiments conducted in a laboratory maintained at 30 °C.

## 2.2. *In vitro* evaluating the antifungal effects of chemical fungicides and *S. philanthi* against *P. salaccae* SKRU002

### 2.2.1. Chemical fungicides effect

The evaluation of these five chemical fungicides against *P. salaccae* SKRU002 was conducted to assess their impact on fungal growth plates, following the method outlined by Droby et al. (2003) [57] with some modifications. In summary, the chemical fungicides, both at 500 and 1000  $\mu\text{L mL}^{-1}$ , were aseptically mixed with melted sterile PDA to achieve a final volume of 10 mL. An equivalent volume of distilled sterile water mixed with melted sterile PDA served as the control. A 5 mm diameter plug of mycelia was excised from a 3-day-old colony of *P. salaccae* SKRU002 and placed at the center of the test agar plates. The cultures were then incubated at 30 °C for 7 days. Afterward, the colony size in each treatment was measured, and the percentage inhibition of hyphal growth was calculated using the following formula (Eq. (1)) [58]:

$$\text{Inhibition of hyphal growth (\%)} = \left[ \frac{\text{Colony diameter of SKRU002 in the control treatment} - \text{Colony diameter of SKRU002 in the chemical fungicide treatment}}{\text{Colony diameter of SKRU002 in the control treatment}} \right] \times 100. \quad (1)$$

The experiment was conducted with three replications.

### 2.2.2. *Streptomyces philanthi* effects

**2.2.2.1. Dual culture effect.** The impact of both strains of *S. philanthi* on *P. salaccae* SKRU002 was assessed using a dual culture assay. Experimental protocols for evaluating antifungal activity were adopted from the procedures outlined by Boukaew and Prasertsan (2014) [44]. In the following seven days of incubation at 30 °C, fungal colony diameters were measured, and the percentage inhibition of hyphal growth for *P. salaccae* SKRU002 was determined using the aforementioned methodology. The experiment was conducted with three replications.

**2.2.2.2. Volatile organic compounds effect.** The study focused on assessing the impact of volatile organic compounds (VOCs) produced by two strains of *S. philanthi* on the mycelial development of *P. salaccae* SKRU002. For each strain of *S. philanthi*, a spore suspension at a concentration of  $10^7$  spores  $\text{mL}^{-1}$  was streaked onto PDA medium in a Petri dish [46]. After a 10-day incubation at 30 °C, a Petri dish containing *S. philanthi* was covered with another Petri dish inoculated with a 5 mm-diameter mycelial plug of *P. salaccae* SKRU002 on PDA medium. The two plates were then sealed with double layers of parafilm to create a double-plate chamber [59]. After seven days of incubation at 30 °C, the fungal colony diameters were measured, and the percentage inhibition of hyphal growth for *P. salaccae* SKRU002 was determined using the previously described method. The experiment was conducted with three replications.

**2.2.2.3. Culture filtrates effect.** A 5 mm-diameter mycelial plug of *P. salaccae* SKRU002 was inoculated at the center of a 9 cm-diameter Petri dish containing PDA mixed with different dilutions (1/10, 1/100, and 1/1000) of BCF RM-1-138 or RL-1-178, prepared using sterile distilled water. Additionally, autoclaved BCF RM-1-138 or RL-1-178 at 121 °C for 15 min was also investigated. Sterile distilled water-treated PDA medium serves as the control. Following the seven days of incubation at 30 °C, the diameters of the fungal colonies were measured, and the percentage inhibition of hyphal growth for *P. salaccae* SKRU002 was calculated employing the method described earlier. The experiment was conducted with three replications.

## 2.3. Comparison of mycelial growth suppression of *P. salaccae* SKRU002 in liquid culture using *S. philanthi* BCF and five chemical fungicides

The efficacy of BCF RM-1-138 and RL-1-178, along with the five chemical fungicides, against *P. salaccae* SKRU002 was investigated. Subsequently, each BCF and chemical fungicide, in a volume of 1 mL, was added to 49 mL of potato dextrose broth (PDB) in 250 mL flasks. A 5 mm diameter mycelial plug extracted from a 3-day-old *P. salaccae* SKRU002 colony was then transferred onto each flask. The flasks were placed in a rotary shaker at 30 °C and 150 rpm for 7 days. Following incubation, the mycelial mats were filtered through preweighed, dried filter paper and dried at 60 °C for 3 days before being weighed. The percentage inhibition of hyphal growth was determined as previously outlined. The experiment was conducted with three replications.

### 2.4. Evaluation of *S. philanthi* BCF and five chemical fungicides for protecting snake fruit from *P. salaccae* SKRU002 and preserving fruit quality

The investigation aimed to assess the potential of five chemical fungicides as well as the BCF of both strains of *S. philanthi* in preventing snake fruit from *P. salaccae* SKRU002. Prepared snake fruits were soaked in each of the chemical fungicides and *S. philanthi* BCF for 10 min at 30 °C. To serve as a control, snake fruits were soaked in sterile distilled water. Afterward, they were dried in a laminar airflow for 30 min before being placed individually inside separate sterile plastic containers measuring  $19.2 \times 28.0 \times 10.9 \text{ cm}^3$ . These containers were maintained under conditions of 90–95 % relative humidity. The snake fruits were then gently wounded using sterile fine needles, and a 5 mm-diameter mycelial plug of *P. salaccae* SKRU002 was inoculated at the center of each fruit. They were subsequently stored at 30 °C for 12 days. After the designated storage period, disease incidence (DI) was assessed by calculating the percentage of rotten snake fruit using the following formula (Eq. (2)) [60]:

$$\text{Disease incidence (\%)} = \left( \frac{\text{Number of rotten snake fruit}}{\text{Total number of snake fruit}} \right) \times 100. \quad (2)$$

Disease severity (DS) was also evaluated after the storage period using a 0-to-4 scale: 0 = no rot; 1 = 1–25% of snake fruit with rot; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%. The DS index was determined using the following formula (Eq. (3)) [60]:

$$\text{Disease severity (\%)} = \left[ \frac{\sum (\text{number of snake fruit in each category} \times \text{corresponding disease scale})}{\text{total number of snake fruit examined} \times \text{highest disease scale}} \right] \times 100. \quad (3)$$

Each treatment involved three replications, with each replication consisting of 10 fruits.

To assess the preservation quality of snake fruit following treatment with *S. philanthi* BCF, five chemical fungicides, and subsequent inoculation with a pathogen, and several parameters were measured over a 12-day storage period. These included pH, color, weight, total soluble solids (TSS), titratable acidity (TA), total phenolic content (TPC), anti-oxidant activity (AA), and sugar components (glucose, sucrose, and fructose). Each treatment was replicated three times, with 10 fruits per replication.

The snake fruit was sampled and weighed using an electronic balance. Weight loss was calculated using the following formula (Eq. (4)) [61]:

$$\text{Weight loss (\%)} = \left[ \frac{\text{Fruit weight before storage} - \text{Fruit weight after storage}}{\text{Fruit weight before storage}} \right] \times 100. \quad (4)$$

The color of stored fruit was measured after treatment under various conditions. CIELAB color parameters ( $L^*$ ,  $a^*$ , and  $b^*$ ) were assessed at three random points on the snake fruit peel using a colorimeter (HunterLab, ColorFlex EZ, USA). In this context,  $L^*$  indicated fruit brightness,

$a^*$  denoted the red/green spectrum (negative values indicating green, while positive values indicated redness), and  $b^*$  represented the yellow/blue value, where yellow corresponded to positive values and blue to negative values.

The snake fruit samples were peeled, sliced into small pieces, and hand-pressed to extract juice into a beaker. The juice was then filtered and immediately analyzed for fruit quality parameters, including pH, TSS, TA, TPC, AA, and sugar composition. The pH of the juice was measured using a pH meter (model FE20 - Mettler Toledo), while sugar components were quantified by high-performance liquid chromatography (HPLC) (Agilent 1200) equipped with an Animex HPX-87H (300 mm × 7.8 mm) column (Bio-Rad, Hercules, CA) and a refractive index (RI) detector. The sample was diluted with deionized water, filtered through a 0.22 µm, 13-mm Nylon membrane filter (Sartorius, Goettingen, Germany), and then injected into the chromatograph under the following conditions: column temperature at 65 °C, detector temperature at 50 °C, 5 mM sulfuric acid as the mobile phase at a flow rate of 0.6 mL/min, and an injection volume of 10 µL [62]. TSS content was determined as described by Spinelli et al. (2024) [63], and TA was measured following the protocols of Ranganna (1986) [64] and Kalsi et al. (2023) [65].

The TPC was determined by using the Folin–Ciocalteu method, with Gallic acid employed as the standard equivalent. The TPC content was assessed using a modified method adopted by Derakhshan et al., 2018 [66]. In summary, 100 µL of 2.0 N Folin–Ciocalteu reagent (Sigma–Aldrich, St. Louis, USA) were mixed with 20 µL of diluted snake juice sample. After 3–5 min, 80 µL of 7 % (w/v) sodium carbonate solution was added to the mixture, and the reaction proceeded for 30 min at room temperature in the dark. The absorbance was measured using a spectrophotometer at 760 nm [67].

The method proposed by Barreca et al. (2011) [68] was employed to assess the AA using 2,2-diphenyl-1-picrylhydrazyl radicals (DPPH), with minor adjustments. Initially, 1.18 mg of DPPH was dissolved in 25 mL of methanol to create the DPPH solution. Subsequently, 100 µL of DPPH solution was mixed with snake juice (100 µL) and then incubated for 30 min at room temperature in the dark. Additionally, a control, 100 µL of methanol solution, was used instead of a snake juice sample. The absorbance was measured at 517 nm using a spectrophotometer, and the result was calculated using the following formula (Eq. (5)) [68]:

$$\text{DPPH free radical scavenging activity (\%)} = \left[ \frac{\text{Absorbance of control} - \text{Absorbance of the sample}}{\text{Absorbance of control}} \right] \times 100. \quad (5)$$

## 2.5. Statistical analysis

All the results were calculated as the mean ± standard deviation. The data underwent analyses of variance (ANOVA) using SPSS software version 21 for Windows. Statistical significance was assessed using Tukey's Honestly Significant Difference (HSD) test, with significance set at  $p < 0.05$ .

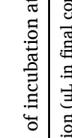
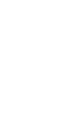
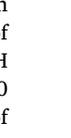
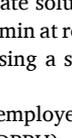
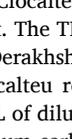
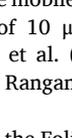
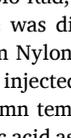
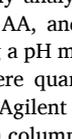
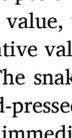
## 3. Results

### 3.1. In vitro evaluating the antifungal effects of chemical fungicides and *S. philanthi* against *P. salacca* SKRU002

#### 3.1.1. Chemical fungicides effect

The effects of different concentrations (0, 500, 1000 µL mL<sup>-1</sup>) of five chemical fungicides on the mycelial growth of *P. salacca* SKRU002 in PDA medium after seven days of incubation at 30 °C were studied and summarized in Table 1. It is clear that an increase in the concentrations of all chemical fungicides significantly ( $p < 0.05$ ) reduced the growth of *P. salacca* SKRU002. Prochloraz® at 1000 µL mL<sup>-1</sup> completely inhibited the growth of *P. salacca* SKRU002 (100 % inhibition), followed by

**Table 1**  
Mycelial growth of *P. salacca* SKRU002 in PDA after seven days of incubation at 30 °C, at distend concentrations of fungicides (prochloraz®, metalaxy®, azoxystrobin®, propiconazole®, and thiram®).

Parameters	Chemical fungicides concentration (µL in final concentration 10 mL PDA)														
	propiconazole®			prochloraz®			metalaxy®			azoxystrobin®			thiram®		
	Control	500	1000	500	1000	500	1000	500	1000	500	1000	500	1000	500	1000
Colony diameter (cm)	9.00 <sup>a</sup> ± 0.00	2.10 <sup>f</sup> ± 0.05	1.55 <sup>g</sup> ± 0.06	0.60 <sup>h</sup> ± 0.27	0.00 <sup>i</sup> ± 0.00	8.88 <sup>a</sup> ± 0.25	7.63 <sup>b</sup> ± 0.25	5.25 <sup>c</sup> ± 0.29	4.38 <sup>d</sup> ± 0.25	3.60 <sup>e</sup> ± 0.12	2.50 <sup>f</sup> ± 0.00	76.67	72.22	60.00	72.22
Inhibition of mycelial growth (%)	-	76.67	82.78	93.33	100.00	1.33	15.22	41.67	51.33	60.00	72.22				
Colony morphology															

Note: The presented data represent the mean of three replicates ± standard deviation (SD). Values within the same row that share the same letter are not considered significantly different, as determined by ANOVA following Tukey's HSD test at a significance level of  $p > 0.05$ .

propiconazole® (82.78 % inhibition), thiram® (72.22 % inhibition), and azoxystrobin® (51.33 % inhibition). However, *P. salacca* SKRU002 showed resistance to metalaxyl®, inhibiting it by only 15.22 %.

### 3.1.2. *Streptomyces philanthi* effects

The dual culture (Fig. 1A and B) and volatile effects (Fig. 1C and D) assays of both strains of *S. philanthi* against *P. salacca* SKRU002 are depicted in Fig. 1. The dual culture showed that both strains RM-1-138 and RL-1-178 inhibited the mycelial growth of *P. salacca* SKRU002 with inhibitions of 80.37 % and 83.33 %, respectively, which was higher than the inhibitions shown by volatile effects at 70.00 % and 68.52 %, respectively. The mycelial growth of *P. salacca* SKRU002 after treatment with both dual culture and volatile assays is depicted in Fig. 1B and D.

The effects of various conditions, including undiluted, 1/10 diluted, 1/100 diluted, 1/1000 diluted, and autoclaved (at 121 °C for 15 min) BCF of strain RM-1-138 (Table 2A) and strain RL-1-178 (Table 2B), on the mycelial growth of *P. salacca* SKRU002 in PDA medium were investigated. Observations were conducted after seven days of incubation at 30 °C and are summarized in Table 2. The study's findings revealed that all treatments significantly ( $p < 0.05$ ) inhibited the growth of *P. salacca* SKRU002. Undiluted BCF of both strain RM-1-138 (73.76 %) and RL-1-178 (76.44 %) exhibited stronger inhibition against *P. salacca* SKRU002 compared to the treated conditions, ranging from 55.56 % to 66.48 % for strain RM-1-138 and from 57.78 % to 66.67 % for strain RL-1-178. Diluted BCF of both strains showed a gradual decrease in inhibition against *P. salacca* SKRU002; however, they still demonstrated inhibitory effects of more than 55 %. Surprisingly, autoclaved BCF of strain RM-1-138 (66.48 %) and strain RL-1-178 (66.67 %) exhibited robust antifungal activity against *P. salacca* SKRU002 compared to the diluted BCF of RM-1-138 (55.56–61.11 %) and RL-1-178 (57.78–64.78 %), suggesting that the BCF possess heat stability. This indicates the potent antifungal effects of both strains in the tested RM-1-138 and RL-1-178 BCF.

### 3.2. Comparison of mycelial growth suppression of *P. salacca* SKRU002 in liquid culture using *S. philanthi* BCF and five chemical fungicides

The antifungal activity of BCF RM-1-138 and RL-1-178 was compared with that of five chemical fungicides on the mycelial growth of *P. salacca* SKRU002 in liquid culture, as summarized in Table 3. The BCF of both strains, RM-1-138 (86.80 %) and RL-1-178 (80.86 %) demonstrated a significantly superior ( $p < 0.05$ ) inhibition of mycelial growth compared to the five chemical fungicides. Specifically, these strains exhibited higher inhibition ( $p < 0.05$ ) than metalaxyl® (9.34 %) and azoxystrobin® (56.84 %), though not significantly ( $p > 0.05$ ) different from thiram® (87.48 %). In contrast, they displayed lower inhibitions compared to propiconazole® and prochloraz®, both achieving 100 % inhibitions. Notably, metalaxyl® (154.73 mg) proved ineffective in inhibiting the mycelial growth of *P. salacca* SKRU002 when compared to the control set (170.67 mg).

### 3.3. Evaluation of *S. philanthi* BCF and five chemical fungicides for protecting snake fruit from *P. salacca* SKRU002

The BCF of both strains of *S. philanthi* and five chemical fungicides were evaluated for their potential to protect against the development of *P. salacca* SKRU002 through *in vivo* assays with snake fruit conducted over 12 days under conditions conducive to fungal proliferation (30 °C and 90–95 % RH). The results, detailed in Table 4 and illustrated in Fig. 2, reveal that the incidence and severity of the disease were calculated based on the percentage of rotten snake fruit. The BCF of both strains of *S. philanthi*, which demonstrated significant ( $p < 0.05$ ) inhibition of mycelial growth in *in vitro* antagonistic assays, was employed to assess their *in vivo* biocontrol efficacy in preventing snake fruit rot caused by *P. salacca* SKRU002. This was compared to the effects of five chemical fungicides.

Soaking snake fruit in the BCF from both strains of *S. philanthi*, as well as in the five chemical fungicides, resulted in a significant ( $p < 0.05$ ) decrease in both DI and DS compared to the control (pathogen

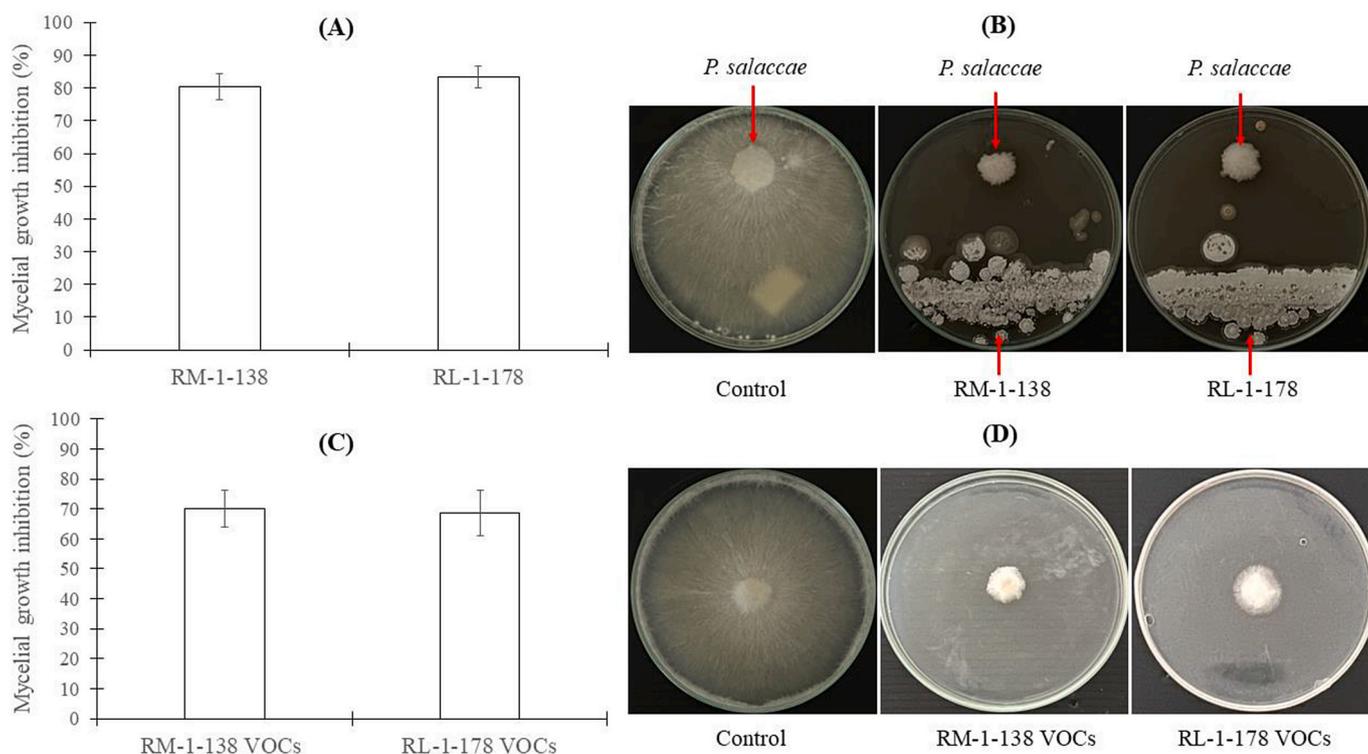
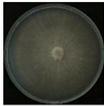
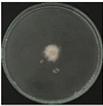
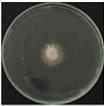
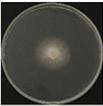
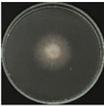
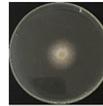
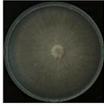
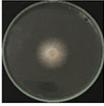
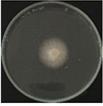
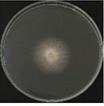
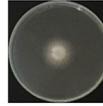


Fig. 1. Antifungal activity of *S. philanthi* strains RM-1-138 and RL-1-178 against *P. salacca* SKRU002 by using dual culture (A and B) and by double plate assay (C and D) on PDA plate after inoculation at 30 °C for seven days.

**Table 2**

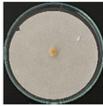
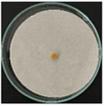
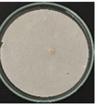
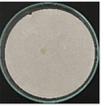
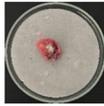
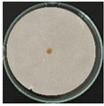
Mycelial growth of *P. salaccae* SKRU002 in PDA after seven days of incubation at 30 °C, in the presence of undiluted, 1/10 diluted, 1/100 diluted, 1/1000 diluted, and autoclaved (at 121 °C for 15 min) BCF RM-1-138 (A) and RL-1-178 (B).

(A)						
Parameters	BCF RM-1-138 (1 mL in 9 mL PDA)					
	Control	Undiluted	1/10 diluted	1/100 diluted	1/1000 diluted	Autoclaved
Colony diameter (cm)	9.00 <sup>a</sup> ± 0.00	2.37 <sup>c</sup> ± 0.38	3.50 <sup>c</sup> ± 0.32	3.75 <sup>bc</sup> ± 0.27	4.00 <sup>b</sup> ± 0.00	3.02 <sup>d</sup> ± 0.04
Inhibition of mycelial growth (%)	–	73.76	61.11	58.33	55.56	66.48
Colony morphology						
(B)						
Parameters	BCF RL-1-178 (1 mL in 9 mL PDA)					
	Control	Undiluted	1/10 diluted	1/100 diluted	1/1000 diluted	Autoclaved
Colony diameter (cm)	9.00 <sup>a</sup> ± 0.00	2.12 <sup>c</sup> ± 0.43	3.17 <sup>cd</sup> ± 0.20	3.52 <sup>bc</sup> ± 0.32	3.80 <sup>b</sup> ± 0.24	3.00 <sup>d</sup> ± 0.06
Inhibition of mycelial growth (%)	–	76.44	64.78	60.89	57.78	66.67
Colony morphology						

Note: The presented data represent the mean of three replicates ± standard deviation (SD). Values within the same row that share the same letter are not considered significantly different, as determined by ANOVA following Tukey's HSD test at a significance level of  $p > 0.05$ .

**Table 3**

Mycelial growth of *P. salaccae* SKRU002 in PDB after seven days of incubation at 30 °C, in the presence of *S. philanthi* BCF (BCF RM-1-138 and RL-1-178) and five chemical fungicides (prochloraz®, metalaxyl®, azoxystrobin®, propiconazole®, and thiram®).

Parameters	Treatments (1 mL in 49 mL PDB)								
	Control	BCF RM-1-138	BCF RL-1-178	propiconazole®	prochloraz®	metalaxyl®	azoxystrobin®	thiram®	
Mycelial dry weight (mg/50 mL)	170.67 <sup>a</sup> ± 4.82	22.53 <sup>c</sup> ± 5.73	32.66 <sup>c</sup> ± 1.51	0.00 <sup>d</sup> ± 0.00	0.00 <sup>d</sup> ± 0.00	154.73 <sup>a</sup> ± 8.83	73.67 <sup>b</sup> ± 6.33	21.37 <sup>c</sup> ± 1.27	
Inhibition of mycelial growth (%)	–	86.80	80.86	100.00	100.00	9.34	56.84	87.48	
Mycelial mats morphology									

Note: The presented data represent the mean of three replicates ± standard deviation (SD). Values within the same row that share the same letter are not considered significantly different, as determined by ANOVA following Tukey's HSD test at a significance level of  $p > 0.05$ .

alone). In pathogen-treated fruits, the DI (100 %) and DS (91.25 %) were higher than in all treated conditions. Notably, the best protection for snake fruit, with both DI and DS at 0 %, was achieved following the application of both propiconazole® and prochloraz®.

In terms of biocontrol ability, the BCF from strain RM-1-138 (35.00 % DI and 18.75 % DS) and strain RL-1-178 (30.00 % DI and 21.25 % DS) provided protection to snake fruit that was not significantly different ( $p > 0.05$ ) from thiram® (40.00 % DI and 23.75 % DS), but was more effective than azoxystrobin® (80.00 % DI and 36.25 % DS). Disease suppression in the treated fruits was 65.00 % and 70.00 % using BCF RM-1-138 and RL-1-178, respectively, compared to the pathogen-inoculated controls (Table 4). On the other hand, metalaxyl® exhibited low protection for snake fruit, with only 5.00 % disease suppression.

Disease symptoms of the entire snake fruit, both externally (Fig. 2A–I) and upon cross-sectioning (Fig. 2J–R), are depicted in Fig. 2. The external symptoms of the negative control (inoculated with pathogen alone) (Fig. 2B) showed the snake fruit covered with fungus, and the fungal hyphae exhibited a yellowish-white color. Cross-sectioned samples showed shrunken skin and pulp with a brown to dark color, indicative of rotten disease (Fig. 2K). However, when both strains of *S. philanthi* and the chemical fungicides (except metalaxyl®) were applied, the cross-sectioned samples showed a significant reduction in rot disease (Fig. 2L–R) compared to the control.

### 3.4. Assessing the quality of snake fruit post-treatment with *S. philanthi* BCF and five chemical fungicides, followed by inoculation with *P. salaccae* SKRU002

The findings demonstrated significant improvements ( $p < 0.05$ ) in various quality parameters, including color, weight, TSS, TPC, AA, and sugar components in snake fruit post-inoculation with *P. salaccae* SKRU002 and treatment with BCF of both strains of *S. philanthi*, alongside five chemical fungicides. These biological and chemical control approaches were employed to assess fruit quality preservation over a 12-day storage period under humid conditions, as detailed in Table 5 and depicted in Fig. 3.

As indicated in Table 5, the positive control, where *P. salaccae* SKRU002 was solely inoculated on snake fruit, exhibited alterations in color parameters ( $L^*$ ,  $a^*$ , and  $b^*$ ) of the snake fruit pulp. However, snake fruit treated with both biological and chemical (propiconazole®, prochloraz®, and azoxystrobin®) control methods, and infected with the pathogen, did not significantly alter ( $p > 0.05$ ) the snake fruit pulp color parameters ( $a^*$  and  $b^*$ ) compared to the negative control with no treatment. Furthermore, the sole inoculation of *P. salaccae* SKRU002 in snake fruit (as a positive control) led to a notably higher loss of 13.28 %, with snake fruit treated with metalaxyl® following closely at 10.90 %. Nevertheless, all treatments exhibited no statistically significant

**Table 4**

Effects of *S. philanthi* BCF (RM-1-138 and RL-1-178) and chemical fungicides (prochloraz®, metalaxyl®, azoxystrobin®, propiconazole®, and thiram®) on snake fruit rot caused by *P. salaccae* SKRU002 after 12 days at 30 °C under humid conditions.

Treatments	Disease incidence (%)	Disease suppression (%)	Disease severity (%)
Control (negative control)	–	–	–
Pathogen alone (positive control)	100.00 <sup>a</sup> ± 0.00	–	91.25 <sup>a</sup> ± 7.07
Pathogen + BCF RM-1-138	35.00 <sup>c</sup> ± 1.07	65.00	18.75 <sup>c</sup> ± 1.27
Pathogen + BCF RL-1-178	30.00 <sup>c</sup> ± 3.24	70.00	21.25 <sup>c</sup> ± 1.84
Pathogen + propiconazole®	0.00 <sup>d</sup> ± 0.00	100.00	0.00 <sup>d</sup> ± 0.00
Pathogen + prochloraz®	0.00 <sup>d</sup> ± 0.00	100.00	0.00 <sup>d</sup> ± 0.00
Pathogen + metalaxyl®	95.00 <sup>ab</sup> ± 7.07	5.00	42.50 <sup>b</sup> ± 1.77
Pathogen + azoxystrobin®	80.00 <sup>b</sup> ± 4.17	20.00	36.25 <sup>b</sup> ± 2.12
Pathogen + thiram®	40.00 <sup>c</sup> ± 1.14	60.00	23.75 <sup>c</sup> ± 1.26

Note: Disease incidence and disease severity were calculated based on rotten snake fruit disease. The presented data represents the mean of three replicates ± standard deviation (SD) (n = 30 per treatment). Values within the same column that share the same letter are not considered significantly different, as determined by ANOVA following Tukey's HSD test at a significance level of  $p > 0.05$ .

variance ( $p > 0.05$ ) in weight loss compared to the negative control (no treatment applied).

In the negative control (no treatment applied), TSS in snake fruit juice measured 13.87 °Brix, while inoculation of *P. salaccae* SKRU002 on snake fruit alone reduced TSS to 8.33 °Brix. However, snake fruit treated with both biological and chemical control methods exhibited preserved TSS levels following *P. salaccae* SKRU002 infection, ranging from 13.00 to 13.67 °Brix and 10.00 to 12.87 °Brix, respectively. Additionally, the TA of snake fruit juice showed no significant difference ( $p > 0.05$ ) (Table 3).

Similarly, in the negative control (no treatment applied), TPC in snake fruit juice was recorded at 129.29 µg GAE/mL. However, inoculation of *P. salaccae* SKRU002 on snake fruit alone and application of metalaxyl® resulted in significant ( $p < 0.05$ ) decreases in TPC to 94.76 µg GAE/mL and 74.32 µg GAE/mL, respectively. Snake fruit treated with both biological and chemical control methods exhibited preserved TPC levels following *P. salaccae* SKRU002 infection, ranging from 142.26 to 147.91 µg GAE/mL and 135.74–260.22 µg GAE/mL, respectively. Notably, the prochloraz® treatment showed the highest preservation rate at 260.22 µg GAE/mL (Table 3).

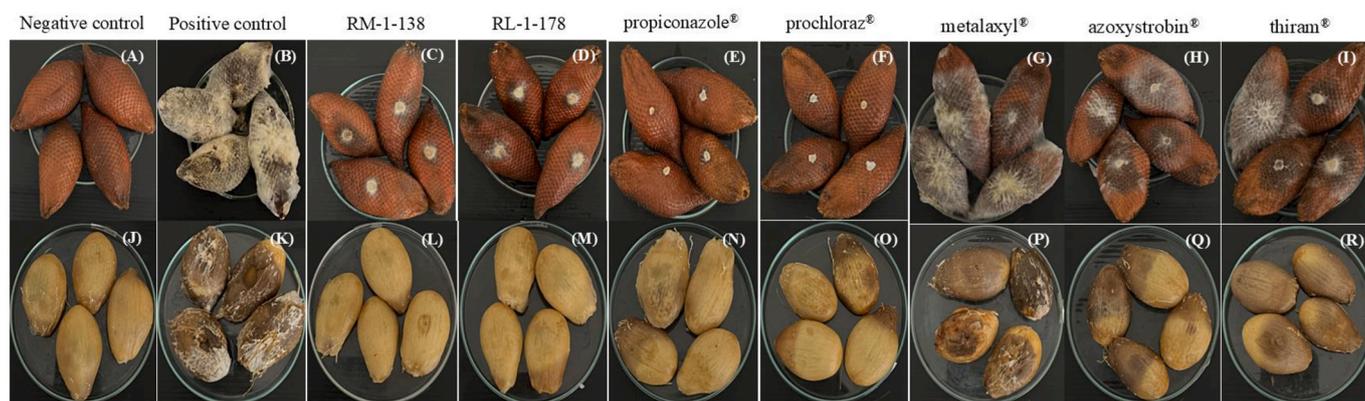
In Table 5, the negative control (no treatment applied) revealed AA in snake fruit juice at 81.09 %RSV. However, in the positive control where *P. salaccae* SKRU002 was inoculated on snake fruit alone, AA significantly decreased to 44.51 %RSV ( $p < 0.05$ ), followed by the application of metalaxyl® (57.76 %RSV). Snake fruit treated with both biological and chemical control methods exhibited preserved AA levels following *P. salaccae* SKRU002 infection, ranging from 82.33 to 83.47 %RSV and 84.03 to 92.98 %RSV, respectively. Notably, the prochloraz® treatment demonstrated the highest preservation rate at 92.98 %RSV.

Sugars are essential compounds in the fruit, influencing the overall taste of snake fruit juice. Therefore, fluctuations in glucose, sucrose, and fructose levels in treated snake fruit throughout the storage period were investigated. As depicted in Fig. 3, in the negative control (no treatment applied), glucose, sucrose, and fructose contents in snake fruit juice were measured at 33.56, 42.12, and 44.66 g L<sup>-1</sup>, respectively. Following sole pathogen inoculation (positive control), glucose (16.35 g L<sup>-1</sup>), sucrose (1.17 g L<sup>-1</sup>), and fructose (36.37 g L<sup>-1</sup>) contents in snake fruit juice were significantly ( $p < 0.05$ ) reduced. However, snake fruit treated with both biological and chemical control methods exhibited significant ( $p < 0.05$ ) preservation of sugar content post- *P. salaccae* SKRU002 infection. Notably, the application of metalaxyl® showed no significant preservation effect ( $p > 0.05$ ) on sucrose concentration (1.72 g L<sup>-1</sup>) compared to the positive control.

#### 4. Discussion

Chemical and biological control methods have been widely applied for managing plant pathogens worldwide, offering diverse strategies to combat diseases effectively while minimizing environmental impacts. Chemical control involves the application of synthetic fungicides, which have demonstrated efficacy in inhibiting fungal growth. Biological control methods, employing beneficial microorganisms, offer sustainable alternatives by harnessing natural antagonistic mechanisms. This study investigates the effectiveness of chemical synthetic fungicides, such as propiconazole®, prochloraz®, metalaxyl®, azoxystrobin®, and thiram®, along with biological controls employing beneficial microorganisms like *S. philanthi* strains RM-1-138 and RL-1-178, against rotten snake fruit caused by *P. salaccae* SKRU002. Overall, the results demonstrate that both chemical and biological control methods successfully managed *P. salaccae* SKRU002 in snake fruit without compromising fruit quality preservation. This research provides valuable insights into the efficacy of chemical treatments and the utilization of beneficial microorganisms in eliminating disease-causing fungi in snake fruit.

While industrial fungicides represent a robust approach to managing plant pathogenic fungi, it's essential to acknowledge their



**Fig. 2.** Protection efficacy of BCF from *S. philanthi* strains RM-1-138 and RL-1-178, as well as five chemical fungicides (prochloraz®, metalaxyl®, azoxystrobin®, propiconazole®, and thiram®), against *P. salaccae* SKRU002 on the symptoms of (A–I) whole snake fruit and, upon cross-sectioning, on (J–R) whole snake fruit after a 12-day storage period at 30 °C under humid conditions.

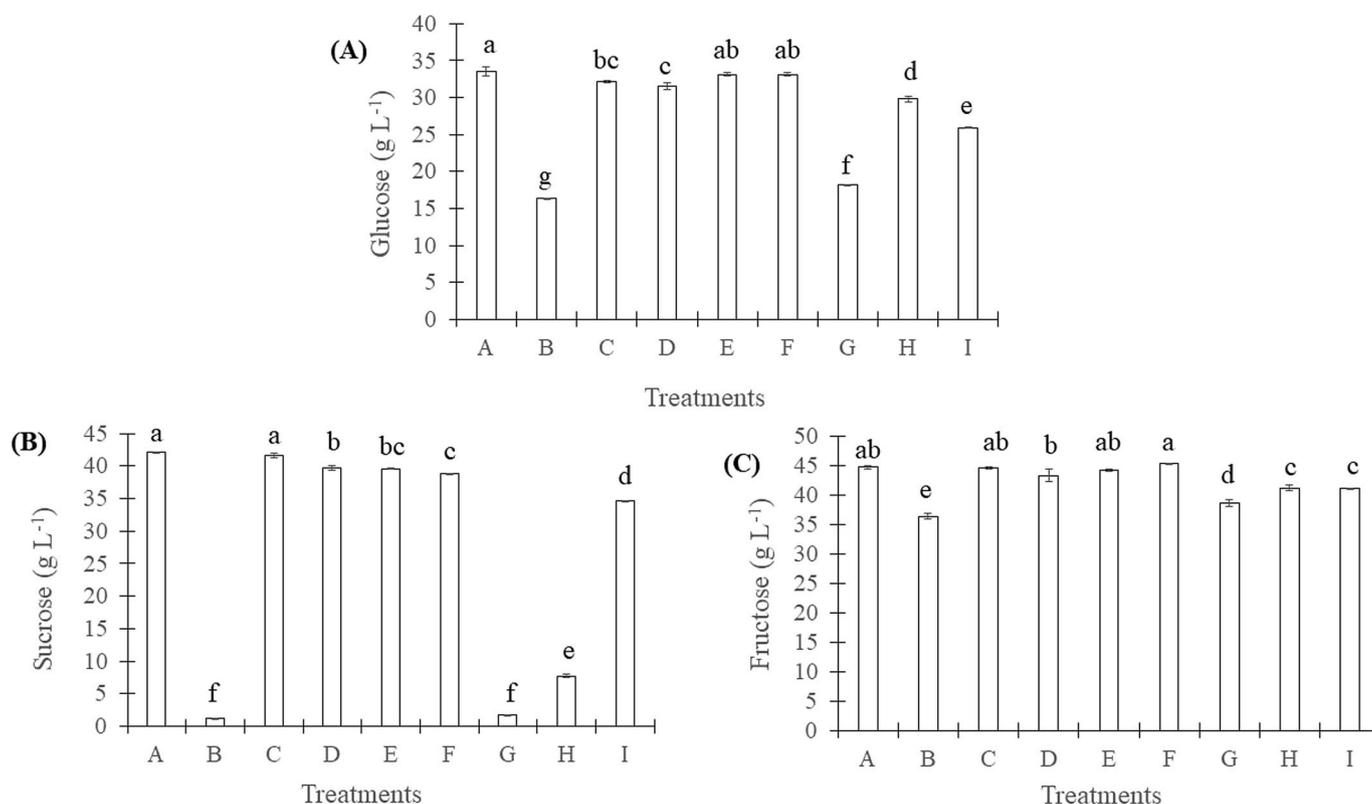
Note: The negative control means no treatment was applied, and the pathogen was not inoculated.

**Table 5**

Quality of snake fruit treated with *S. philanthi* BCF (BCF RM-1-138 and RL-1-178) or chemical fungicides (prochloraz®, metalaxyl®, azoxystrobin®, propiconazole®, and thiram®) after inoculation with *P. salaccae* SKRU002, following 12 days at 30 °C under humid conditions.

Treatments	pH	Color			Weight loss (%)	Total soluble solids (°Brix)	Titratable acidity (% citric acid)	Total phenol content (µg GAE/mL)	% Radical scavenging activity
		L*	a*	b*					
Control (negative control)	4.16	62.84 <sup>a</sup>	8.32 <sup>c</sup>	32.29 <sup>a</sup>	5.45 <sup>c</sup> ± 0.50	13.87 <sup>a</sup> ± 0.23	0.28 <sup>ab</sup> ± 0.01	129.29 <sup>c</sup> ± 20.56	81.09 <sup>b</sup> ± 1.37
Pathogen alone (positive control)	3.66	28.10 <sup>e</sup>	11.00 <sup>a</sup>	19.92 <sup>e</sup>	13.28 <sup>a</sup> ± 0.83	8.33 <sup>f</sup> ± 0.12	0.26 <sup>a</sup> ± 0.00	94.76 <sup>d</sup> ± 18.87	44.51 <sup>e</sup> ± 4.46
Pathogen + BCF RM-1-138	3.96	62.78 <sup>a</sup>	8.49 <sup>c</sup>	32.30 <sup>a</sup>	5.75 <sup>c</sup> ± 0.17	13.67 <sup>ab</sup> ± 0.42	0.29 <sup>ab</sup> ± 0.01	142.26 <sup>c</sup> ± 3.82	82.33 <sup>b</sup> ± 1.93
Pathogen + BCF RL-1-178	3.78	61.95 <sup>a</sup>	8.53 <sup>c</sup>	32.29 <sup>a</sup>	5.90 <sup>c</sup> ± 0.21	13.00 <sup>bc</sup> ± 0.00	0.29 <sup>ab</sup> ± 0.00	147.91 <sup>c</sup> ± 7.46	83.47 <sup>b</sup> ± 0.39
Pathogen + propiconazole®	3.63	57.91 <sup>b</sup>	8.48 <sup>c</sup>	33.28 <sup>a</sup>	5.31 <sup>c</sup> ± 0.02	11.67 <sup>d</sup> ± 0.12	0.34 <sup>abc</sup> ± 0.01	232.19 <sup>b</sup> ± 8.01	84.26 <sup>b</sup> ± 0.52
Pathogen + prochloraz®	3.59	57.18 <sup>b</sup>	8.50 <sup>c</sup>	32.31 <sup>a</sup>	5.73 <sup>c</sup> ± 0.29	12.87 <sup>c</sup> ± 0.23	0.38 <sup>abc</sup> ± 0.02	260.22 <sup>a</sup> ± 30.19	92.98 <sup>a</sup> ± 1.36
Pathogen + metalaxyl®	3.47	37.99 <sup>d</sup>	10.26 <sup>b</sup>	20.30 <sup>d</sup>	10.90 <sup>b</sup> ± 1.15	10.00 <sup>e</sup> ± 0.00	0.44 <sup>a</sup> ± 0.01	74.32 <sup>d</sup> ± 8.29	57.76 <sup>d</sup> ± 0.78
Pathogen + azoxystrobin®	3.54	47.03 <sup>c</sup>	8.41 <sup>c</sup>	26.35 <sup>b</sup>	5.98 <sup>c</sup> ± 0.20	10.33 <sup>e</sup> ± 0.23	0.38 <sup>ab</sup> ± 0.02	135.74 <sup>c</sup> ± 6.96	69.76 <sup>c</sup> ± 2.59
Pathogen + thiram®	3.49	45.15 <sup>c</sup>	8.47 <sup>c</sup>	25.54 <sup>c</sup>	5.99 <sup>c</sup> ± 0.19	11.13 <sup>d</sup> ± 0.42	0.33 <sup>abc</sup> ± 0.02	220.37 <sup>b</sup> ± 3.77	84.03 <sup>b</sup> ± 0.59

Note: The presented data represents the mean of three replicates ± standard deviation (SD) (n = 30 per treatment). L\* indicated fruit brightness, a\* denoted the red/green spectrum (negative values indicating green, while positive values indicated redness), and b\* represented the yellow/blue value, where yellow corresponded to positive values and blue to negative values. Values within the same column that share the same letter are not considered significantly different, as determined by ANOVA following Tukey's HSD test at a significance level of  $p > 0.05$ .



**Fig. 3.** Depicts the comprehensive analysis of glucose (A), sucrose (B), and fructose (C) quality in snake fruit. The fruit was treated with BCF of *S. philanthi* strains RM-1-138 and RL-1-178, in conjunction with five chemical fungicides (prochloraz®, metalaxyl®, azoxystrobin®, propiconazole®, and thiram®), and inoculated with the pathogen. This was done following a 12-day storage period at 30 °C under humid conditions. Notably, the experiment includes various treatments: (A) Control (negative control); (B) Pathogen alone (positive control); (C) Pathogen + BCF RM-1-138; (D) Pathogen + BCF RL-1-178; (E) Pathogen + propiconazole®; (F) Pathogen + prochloraz®; (G) Pathogen + metalaxyl®; (H) Pathogen + azoxystrobin®; (I) Pathogen + thiram®. The presented values reflect the mean (±SD) of three replicates, and statistically nonsignificant differences are denoted by identical letters, as determined by Tukey's HSD test in ANOVA ( $p > 0.05$ ).

environmental impact and potential for fungicide resistance development. Despite these drawbacks, the application of chemical solutions remains vital for proactive disease prevention and minimizing economic

losses in crop production. The *in vitro* chemical fungicides test highlighted the robust protective effect of prochloraz® in inhibiting the mycelial growth of *P. salaccae* SKRU002 on PDA, surpassing

propiconazole®, azoxystrobin®, and thiram®. Propiconazole® and prochloraz® demonstrated higher efficacy compared to other tested fungicides, offering insights for optimizing disease management strategies and emphasizing the importance of a balanced and sustainable approach in crop protection practices.

Our investigation further evaluated the inhibitory effects of both strains of *S. philanthi* on the mycelial growth of *P. salaccae* SKRU002. Findings from both the dual culture method and volatile assay on PDA plates indicated a robust direct antifungal effect, with both strains inhibiting *P. salaccae* SKRU002 by more than 68.52 %. This highlights the potent antifungal properties of these *Streptomyces* strains.

Moreover, the BCF from both strains of *S. philanthi*, tested under various conditions, demonstrated significant inhibition of *P. salaccae* SKRU002. Notably, this inhibition surpassed the effectiveness of widely used fungicides such as metalaxyl® and azoxystrobin® and was equivalent to thiram®. However, it is important to note that the observed inhibition was comparatively lower than that achieved with propiconazole® and prochloraz®.

These results suggest that the antifungal activity of *S. philanthi* strains involves both direct interactions, as seen in the dual culture and volatile assays, and the production of inhibitory compounds present in the culture filtrates. The effectiveness of these strains, particularly in comparison to standard chemical fungicides, underscores their potential as promising biocontrol agents. While the observed inhibition may vary under different conditions, the overall efficacy of *S. philanthi* strains against *P. salaccae* SKRU002, as demonstrated in this study, offers valuable insights into natural and sustainable alternatives for fungal disease management. A comparative analysis of chemical fungicides provides context for understanding the potential of *S. philanthi* in integrated pest management strategies, emphasizing their role as effective contributors to antifungal activities in agriculture.

The application of both strains of *S. philanthi*, along with five chemical fungicides, showed significant efficacy in protecting snake fruit against *P. salaccae* SKRU002. The BCF of *S. philanthi* RM-1-138 and RL-1-178 effectively reduced disease incidence (65.00 % for RM-1-138 and 70.00 % for RL-1-178) and disease severity (18.75 % for RM-1-138 and 21.25 % for RL-1-178) in infected fruit during a 12-day incubation period. These results surpassed the effects of metalaxyl®, azoxystrobin®, and thiram®.

Among the chemical fungicides tested, propiconazole® and prochloraz® were the most effective, achieving complete disease suppression (100 %). This aligns with recent studies showing prochloraz®'s efficacy in controlling *Alternaria alternata* and *C. gloeosporioides* in mango fruit [69], as well as *Curvularia lunata* in habanero pepper [70]. Propiconazole® has also been effective in reducing *Botryodiplodia theobromae* lesions in mango fruit [71]. Prochloraz®, an imidazole fungicide widely used in agriculture, consistently inhibits fungal growth, further supporting its role in integrated disease management strategies [72]. In this study, prochloraz® and propiconazole® were the most effective fungicides, followed by thiram®, azoxystrobin®, and metalaxyl®. The varying efficacy of these fungicides can be attributed to their distinct modes of action. Both prochloraz® and propiconazole® are azole-based fungicides that inhibit ergosterol biosynthesis, a key component of fungal cell membranes, leading to cell death [73,74].

Thiram®, a dithiocarbamate fungicide, inhibits spore germination by disrupting enzyme activity [75], making it effective as a preventive treatment, though less effective once fungal growth is established. Azoxystrobin®, a strobilurin fungicide, inhibits mitochondrial respiration in fungi [76], but its moderate efficacy in this study may be due to *P. salaccae*'s tolerance to this mechanism. Metalaxyl®, a phenylamide fungicide, primarily targets oomycetes by inhibiting RNA synthesis [77], explaining its lower efficacy against true fungi like *P. salaccae* SKRU002. The results suggest that the varying efficacy of these fungicides is directly related to their modes of action. Azole-based fungicides (prochloraz® and propiconazole®) outperform others due to their targeted disruption of fungal cell membranes, whereas fungicides like thiram®

and azoxystrobin®, which rely on broader biochemical disruptions, offer only moderate control. Metalaxyl®'s low efficacy highlights its limited use in managing true fungal pathogens like *P. salaccae* SKRU002.

*Streptomyces* species have garnered attention as effective biocontrol agents against various plant pathogens, showcasing their potential to produce bioactive compounds and inhibit the mycelial growth of numerous fungi [78–83]. This versatility has extended to successful applications in controlling fungal diseases on a variety of fruit crops. For example, fermented extracts of *Streptomyces albiflavine* DSM 42598T significantly reduced postharvest tomato fruit decay caused by *Penicillium citrinum* [80]. Additionally, the polyene macrolide lucensomycin, derived from *Streptomyces plumbeus* strain CA5, demonstrated complete inhibition of gray mold development in grapes caused by *Botrytis cinerea* [78].

*Streptomyces violascens* MT7 extracellular metabolites were also found to be effective in biological control, reducing diseases caused by *Geotrichum candidatum* and *Rhizopus stolonifer* on oranges and papaya fruits [82]. Furthermore, the volatiles of *Streptomyces salmonis* PSRDC-09 displayed high antifungal activity against *Colletotrichum* species, as demonstrated by Boukaew et al. (2021) [84]. In a recent study by Li et al. (2024) [83], the volatiles of *Streptomyces corchorusii* CG-G2 exhibited remarkable efficacy in inhibiting fruit decay and preserving fruit quality in strawberries affected by anthracnose caused by *C. gloeosporioides*.

In the context of this study, both strains RM-1-138 and RL-1-178 have proven to be broad-spectrum and effective agents in controlling various pathogens across different crops. This includes *S. rolfii* and *R. solanacearum* on chili [41], *R. solani* on rice [42–45], *B. cinerea* on tomatoes [46,47], *A. parasiticus* and *A. flavus* on maize seeds [48–53], *C. gloeosporioides* on chili fruit [54], *P. digitatum* on orange [55], and *C. oryzae* on oil palm leaf segments [56]. The findings from this study validate the broad and effective suppressive capabilities of both strains, affirming their utility across a diverse spectrum of pathogens relevant to agricultural applications. This comprehensive approach to disease management presents a promising avenue for sustainable and effective strategies in snake fruit cultivation.

The evaluation of fruit and vegetable quality emerges as a pivotal factor in understanding the implications of storage and their economic significance. Essential parameters such as weight loss rate, TSS, TA, TPC, AA, and sugar composition serve as fundamental indicators of fruit quality [85]. Our study's findings underscore the efficacy of both strains of *S. philanthi*, as well as five chemical fungicides, not only in providing significant protection against *P. salaccae* SKRU002-induced damage in snake fruit but also in effectively preserving its overall quality. Notably, snake fruit treated with both biological and chemical control methods exhibited elevated levels of TSS, TA, TPC, AA, and sugar components compared to the positive control (snake fruit solely inoculated with the pathogen).

Moreover, the BCF from both strains of *S. philanthi* inhibited the growth of *P. salaccae* SKRU002 *in vitro*, without eliciting significant differences in weight loss compared to the negative control (no treatment applied). Likewise, no discernible changes in TSS, TA, TPC, AA, and sugar content of snake fruit were observed in 12 days, suggesting that both culture filtrates did not adversely affect fruit quality. These results align with the findings of postharvest strawberry fruit treated with *Streptomyces* sp. H4 extracts, exhibited preserved TSS, TA, and firmness against *Colletotrichum fragariae* [86].

Furthermore, among the chemical treatments, metalaxyl® demonstrated ineffectiveness in preventing pathogen growth, resulting in significantly higher fruit weight loss of 10.90 %. Similarly, noticeable alterations in TSS, TPC, AA, and sugar content of snake fruit were observed at 12 days, indicating metalaxyl®'s inefficacy in protecting snake fruit from *P. salaccae* SKRU002-induced damage. These declines in quality parameters were attributed to infection by phytopathogenic fungi. This inference finds support in the fact that BCF of *S. philanthi* strains and certain chemical fungicide treatments efficiently inhibited

*P. salacca* SKRU002 growth and mitigated the deterioration of fruit quality.

## 5. Conclusion

Investigations into chemical and biological control methods, including *S. philanthi* strains and five commercial fungicides, revealed promising results against rotten snake fruit caused by *P. salacca* SKRU002. Notably, prochloraz® exhibited complete inhibition of *P. salacca* SKRU002, surpassing other fungicides. Biological control with both strains of *S. philanthi* showed significant inhibition of *P. salacca* SKRU002, attributed to synergistic compound production. The comparative analysis highlighted the superior inhibition rates of biological control over certain chemical fungicides. Untreated snake fruit showed high disease incidence and severity induced by *P. salacca* SKRU002. However, the application of both strains of *S. philanthi*, along with three chemical fungicides (propiconazole®, prochloraz®, and azoxystrobin®), effectively controlled the rotten snake fruit without compromising fruit quality. This study offers comprehensive strategies to mitigate fungal-induced losses and ensure snake fruit quality preservation in agricultural practices, contributing valuable insights to the field.

## CRedit authorship contribution statement

**Sawai Boukaew:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Krittin Chumkaew:** Writing – review & editing. **Jaturong Kumla:** Writing – review & editing. **Nakarin Suwannarach:** Writing – review & editing. **Wanida Petlamul:** Writing – review & editing. **Karistsapol Nooprom:** Writing – review & editing. **Julalak Chuprom:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

## Availability of data and materials

Not applicable.

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## Declaration of Competing Interest

The authors declare no competing interests regarding the publication of this study.

## Data availability

The authors do not have permission to share data.

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