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RESEARCH ARTICLE
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Effects of Tapping the *Styrax paralleloneurus* Tree on Indole-3-Acetic Acid Production by the Endophytic Bacterium *Kocuria palustris*

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ABSTRACT

The Toba frankincense tree *(Styrax paralleloneurus*) is valued for its high-quality resin, which is traditionally extracted through stem tapping. This practice induces plant defense mechanisms and may influence the activity of endophytic bacteria, particularly their ability to produce indole-3-acetic acid (IAA), a key phytohormone involved in plant growth. Although the economic and taxonomic aspects of frankincense trees have been well studied, their microbial associations remain underexplored. The aim of this study was to compare IAA production and the characteristics and abundances of endophytic bacteria isolated from tapped and untapped *S. paralleloneurus*. Bacterial isolates were obtained, macroscopically characterized, assessed for IAA production, and taxonomically identified. The results revealed a higher diversity and abundance of endophytes in tapped trees (17 isolates) than in untapped trees (7 isolates). Furthermore, isolates from tapped trees exhibited significantly higher IAA production (14.44ppm) than the isolates from untapped trees (1.13ppm). The highest IAA-producing isolate was identified as *Kocuria palustris*, highlighting the potential role of tapping in fostering beneficial plant–microbe interactions. These findings suggest that tapping may alter the microbial ecology of *S. paralleloneurus* by enhancing tree growth and resilience.

Keywords: Endophytic bacteria, IAA production, *Styrax paralleloneurus*, tapping, *Kocuria palustris*

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INTRODUCTION

Styrax paralleloneurus, commonly known as Toba frankincense, is a valuable medicinal plant native to North Sumatra, Indonesia. This tree yields an oleo-gum resin known as frankincense, which is widely used in the pharmaceutical, cosmetic, and food industries (Lemenith & Teketay, 2005). Beyond its economic significance, the Toba frankincense tree harbors a diverse population of endophytic bacteria contributing to its growth and development (Liu et al., 2017).

Endophytic fungi and bacteria establish close relationships with their host plants, affecting various biological functions such as synthesizing secondary metabolites (Kouipou Toghueo & Boyom, 2019) and essential phytohormones, which can subsequently be absorbed by the host plant, resulting in increased growth and productivity (Nogaye et al., 2018). Some endophytic bacteria produce plant growth hormones such as indole-3-acetic acid (IAA), which stimulates plant growth and development (Nogaye et al., 2018). Additionally, certain endophytic bacteria can solubilize inorganic phosphates, making them more readily available for plant uptake, thereby improving plant nutrient acquisition capabilities (Nogaye et al., 2018; Cappellari et al., 2019). IAA is a natural auxin hormone that regulates key plant processes, including cell division, differentiation, elongation, and root and shoot growth. Botanical research has widely recognized its vital role in plant development.

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Wounding stress in plants can result from various environmental factors, such as herbivory and mechanical damage, including tapping. This stress elicits a series of physiological responses in plants, which involve the production of signaling molecules, such as abscisic acid and IAA (Bharath et al., 2021). Specifically, wounding stress stimulates indole acetic acid (IAA) production in plant tissues, aiding the ability of plants to repair and regenerate damaged areas. The correlation between wounding stress and IAA production is dynamic and multifaceted and involves the interaction of various plant hormones and signaling pathways. Understanding these mechanisms is essential to formulating strategies to enhance plant resilience and productivity in response to environmental stress (Lim et al., 2015; Hu et al., 2016; Bharath et al., 2021).

The practice of tapping *S. paralleloneurus* trees, which are commonly used for extracting frankincense, can have a notable effect on the physiology of the plant and its associated endophytic community. Tapping may trigger stress responses in trees, affect secondary metabolite production, including that of IAA and influence endophytic bacterial activity. IAA-producing endophytic bacteria can enhance Toba frankincense tree growth, boost resin production, and benefit local communities dependent on this resource.

Furthermore, changes in plant physiology and endophytic communities may have implications for the overall fitness and resilience of trees to biotic and abiotic stresses. This study aimed to compare IAA production, examine the differences in their characteristics and abundance, and identify the endophytic bacteria with the highest IAA production from tapped and untapped *S. paralleloneurus* trees.

MATERIALS & METHODS

Sample Collection and Preparation

The collected samples comprised segments of frankincense tree stems from the Dolok Sanggul community forest in Humbang Hasundutan, North Sumatra, Indonesia. The samples included both tapped and untapped stems. The trees selected for sampling were over 10 years old, and both tapped and untapped specimens were included from the representative plots. Bark samples were collected at breast height under aseptic conditions to prevent contamination. Each sample was collected from three biological replicates (Shi et al., 2022).

Isolation and Purification of Endophytic Bacteria

The samples were cut into 1 × 1 cm pieces and subjected to a stepwise sterilization procedure to improve surface sterilization. They were immersed in 75% alcohol for 1min, treated with sodium hypochlorite for 5min, and finally soaked in 75% alcohol for 30s. Subsequently, the samples were rinsed two to four times with distilled water and dried on sterile tissue paper, as described by Si et al. (2022), with slight modifications. The final rinse water serves as a control and is cultured on Nutrient Agar (NA) in Petri dishes, which are incubated at 28 to 30°C for 2 to 3 days. Bacterial colonies on nutrient agar (NA) plates were purified by transferring them to fresh NA media using the sterile loop and quadrant streak techniques. The plates were sealed with plastic wrap to reduce contamination and incubated at room temperature until distinct single colonies appeared (Sangwan et al., 2021).

Indole Acetic Acid (IAA) Production Assay

An IAA standard curve was prepared by diluting 40ppm of L-tryptophan stock to final concentrations of 0–10ppm. Each solution (2mL) was mixed with 2mL of Salkowski's reagent and incubated in the dark for 60min before measuring the absorbance at 530 nm. Endophytic bacteria were cultured in 5mL of nutrient broth with 0.1mL L-tryptophan and incubated at 150rpm for 48 h. After centrifugation (10,000rpm for 10min at 4°C), 2mL of supernatant was combined with 2mL Salkowski's reagent and incubated in the dark for 60min. The absorbance at 530nm confirmed IAA production, as indicated by the pink color. All treatments were conducted in triplicate with biological replicates. IAA concentrations were determined by applying a standard curve equation to a specific formula.

$$y = ax + b$$

y = *Dependent Variabel (absorbance)*
x = *Independent Variable*
a = *constanta*
b = *Coefficient*

Molecular Identification

DNA Isolation

DNA was isolated as previously described by Osborne et al. (2005) with modifications. The samples were purified and incubated for 24h. Following incubation, each sample was transferred into a 1.5mL microtube, with two replicates per sample. The microtubes were then placed in a microwave at approximately 50°C for 15s. The PCR mix was prepared using the 16S rRNA gene with 1492 R and 27 F primers. Two PCR master mixes were used to check for the presence of DNA. The first mix consisted of MyTaq HS DNA Polymerase (5μL), 1492 R primer (0.5μL), 27 F primer (0.5μL), and nuclease-free water (NFW, 19μL). The second mix contained KOD One PCR Master Mix (12.5μL), 1492 R primer (0.75μL), 27 F primer (0.75μL), and NFW (11μL), totaling 25μL per reaction. The PCR mix was added to the sample microtube and amplified for 30 cycles: pre-denaturation at 95°C for 1min, denaturation at 95°C for 30s, annealing at 53°C for 30s, and extension at 72°C for 1min. A final elongation at 72°C for 5min was followed by storage at 4°C.

Agarose gel electrophoresis was performed to validate the amplification results. We dissolved 0.32g of 0.8% agarose in 40mL of TAE buffer, heated it until fully dissolved, and allowed it to cool. After adding 1.5μL of Florosafe DNA stain and mixing, the solution was poured into a mold with a comb to solidify. The solidified agarose was placed in the electrophoresis apparatus, and TAE buffer was added until submerged. A 4μL DNA marker and a 4μL DNA sample were added to each well. Electrophoresis was performed for 25min, and the gel was observed using the Gel Doc tool.

Sequencing and Identification

The PCR products were sequenced using a SeqStudio Genetic Analyzer (Thermo Fisher Scientific). Forward and reverse sequences were quality-checked using BioEdit (v7.2.5.0) and merged into contigs. BLAST analysis (NCBI GenBank) was used to identify sequence similarities, and a phylogenetic tree was constructed using MEGA 11 (Tamura et al., 2021).

Data Analysis

Analysis of variance (ANOVA) was used to conduct data analysis, followed by the Kruskal–Wallis and Dunn tests. Data analysis was conducted using the R statistical program (van Hecke, 2012).

RESULTS

Endophytic Bacteria from *S. paralelloneurus*

Sampling was performed on both tapped and untapped trees within community forests. In total, 23 bacterial isolates were collected: 7 from untapped and 16 from tapped trees. These isolates exhibited variations in characteristics that were assessed through straightforward morphological observations under a microscope (Table 2). Isolates from untapped trees were designated the code TS (Untapped/Tidak Sadap), whereas those from tapped trees were labeled S (Tapped/Sadap) (Fig. 1).

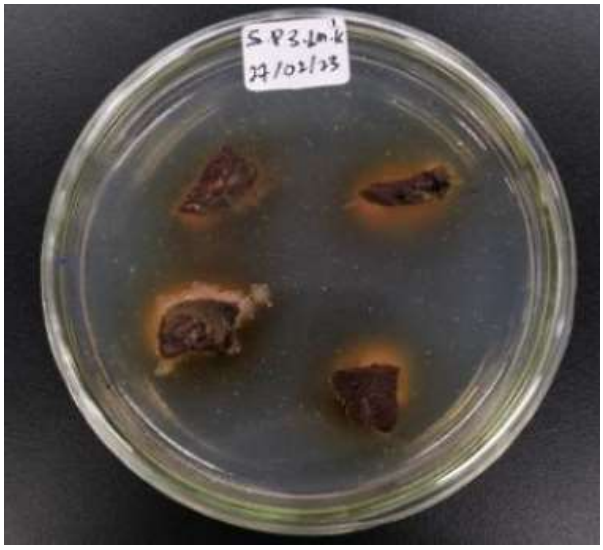

Fig. 1: Isolation of endophytic bacteria from *S. paralleloneurus* stems in NA media, 48 hours post-inoculation.

Endophytic Bacteria Produce Indole-3-acetic Acid (IAA)

The results of the IAA production assay demonstrated distinct color variations among the isolates. The ability of each isolate to produce IAA was evidenced by the color change observed after the addition of the Salkowski reagent. A red or pink hue signifies that the isolate can produce IAA, as exemplified by the isolate that turned pink.

Average IAA production by the bacterial isolates is shown in Table 1. The average IAA production capacity of bacteria from untapped trees (TS) was 1.126286ppm, whereas that from tapped trees (S) was 14.44175ppm (Table 1). The highest IAA concentration was observed in isolate S4, with a value of 26.75ppm, whereas the lowest was observed in isolate TS5, with a value of 0.04ppm. Additionally, the IAA production capacity of each endophyte (Fig. 2) showed that nearly all the endophytic bacteria isolated from the tapped stems produced substantial quantities.

Table 1: Average IAA production by bacterial isolates

Isolate	Absorbance	IAA (ppm)
TS1	0.099	2.708
TS2	0.039	0.973
TS3	0.071	1.898
TS4	0.008	0.078
TS5	0.007	0.049
TS6	0.073	1.956
TS7	0.013	0.222
S.1	0.103	2.823
S.2	0.119	3.286
S.3	0.587	16.812
S.4	0.931	26.754
S.5	0.652	18.690
S.6	0.667	19.124
S.7	0.492	14.066
S.8	0.549	15.713
S.9	0.418	11.927
S.10	0.695	19.933
S.11	0.437	12.476
S.12	0.588	16.841
S.13	0.061	1.609
S.14	0.058	1.523
S.15	0.802	23.026
S.16	0.921	26.465

Table 2: Endophytic bacteria isolated from *S. paralelloneurus*

Isolate	Shape	Elevation	Margin	Colour
TS1	*Circular*	*Flat*	*Entire*	Yellow
TS2	*Circular*	*Flat*	*Entire*	Yellow
TS3	*Circular*	*Flat*	*Entire*	White
TS4	*Circular*	*Convex*	*Entire*	Yellow
TS5	*Circular*	*Flat*	*Entire*	White
TS6	*Circular*	*Flat*	*Entire*	White
TS7	*Rhizoid*	*Flat*	*Lobate*	White
S.1	*Circular*	*Flat*	*Entire*	Yellow
S.2	*Circular*	*Flat*	*Entire*	White
S.3	*Circular*	*Flat*	*Undulate*	White
S.4	*Circular*	*Flat*	*Entire*	Yellow
S.5	*Circular*	*Flat*	*Entire*	White
S.6	*Irreguler*	*Convex*	*Undulate*	Yellow
S.7	*Circular*	*Flat*	*Entire*	Yellow
S.8	*Circular*	*Raised*	*Entire*	White
S.9	*Circular*	*Flat*	*Entire*	Yellow
S.10	*Irreguler*	*Flat*	*Entire*	White
S.11	*Circular*	*Flat*	*Entire*	White
S.12	*Circular*	*Flat*	*Entire*	White
S.13	*Circular*	*Flat*	*Entire*	White
S.14	*Circular*	*Flat*	*Entire*	White
S.15	*Circular*	*Flat*	*Entire*	Yellow
S.16	*Circular*	*Flat*	*Entire*	Yellow

ANOVA produced an F-value of 23.34, indicating a statistically significant difference between the mean values of the treatment groups relative to the variation observed within the groups. Additionally, the *p*-value (Pr > F) was less than the significance level of 0.05, indicating a significant difference between the IAA concentration and treatment (tap and untapped). Therefore, the null hypothesis (h0) was rejected.

```
            Df Sum Sq Mean Sq F value   Pr(>F)
treatment    1  984.7   984.7   23.34 8.94e-05 ***
Residuals   21  886.1    42.2
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

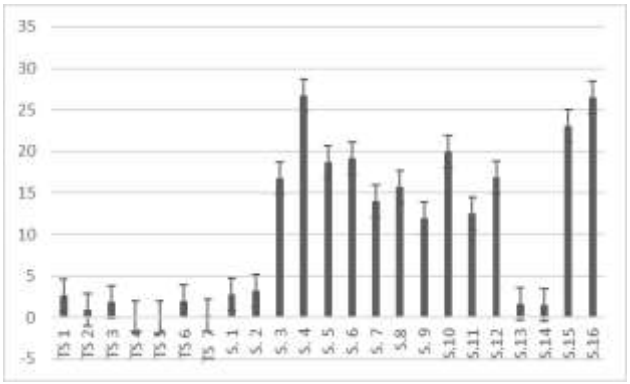

Fig. 2: IAA production by each endophytic bacteria.

In the post-hoc analysis for the Kruskal-Wallis test, the results showed a P-value of 0.0003983, which is below the significance level of 0.05. This indicates a statistically significant difference in IAA concentrations between the treatments (tap and untapped), resulting in rejecting the null hypothesis (H0).

Kruskal-Wallis chi-squared = 12.54, df = 1, p-value = 0.0003983

Kruskal-Wallis rank sum test Dunn Test

data: x and group

Kruskal-Wallis chi-squared = 12.5402, df = 1, p-value = 0

```
Comparison of x by group
      (Bonferroni)

Col Mean-|
Row Mean |      Tapped
---------+-----------
Untapped |   3.541211
         |    0.0002*

alpha = 0.05
Reject Ho if p <= alpha/2
```

Given that the Kruskal-Wallis analysis satisfied the necessary assumptions, a subsequent test using the Dunn Test was conducted. The chi-square value obtained from this test was 12.5402, indicating a significant difference among the groups. Additionally, the p-value from the Dunn Test was 0.0002, reflecting a very strong statistical significance and confirming that the differences between the groups were substantial Fig. 3.

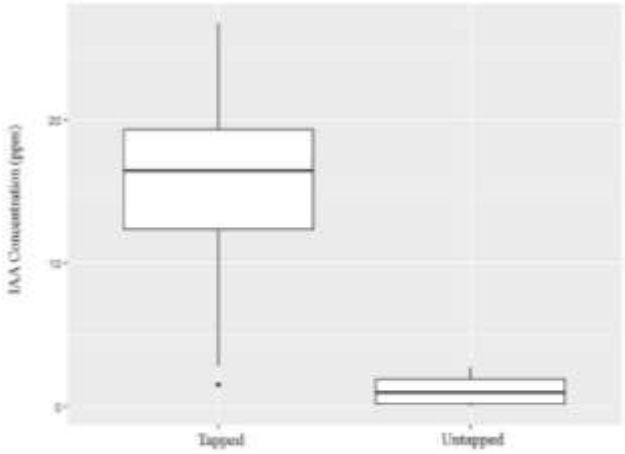

Fig. 3: Average IAA production by endophytic bacteria.

Identification of Potential Endophytic Bacteria

Molecular identification was performed on the bacteria with the highest IAA production capacity. These bacteria were isolated from tapped frankincense tree trunks. Molecular identification established *Kocuria palustris* as the endophytic bacterium exhibiting the highest IAA production, isolated from the tapped tree (Fig. 4), with a query coverage of 99% and 99.42% identity.

DISCUSSION

Plants are continually exposed to various abiotic and biotic stressors that affect physical damage and wound healing. Wounding can activate complex defense mechanisms within plants, producing various secondary metabolites and phytohormones (Benlarbi et al., 2014). One important hormone involved in wound response is IAA, a naturally occurring auxin that plays a crucial role in plant healing and recovery processes. Certain endophytic bacteria residing within plant tissues produce IAA, potentially influencing the physiological responses of plants to wounding (Benlarbi et al., 2014; Pascale et al., 2020). The terpenoid-indole alkaloid pathway is a crucial biosynthetic route for the synthesis of IAA and other defense-related compounds in plants. This pathway is controlled by jasmonic acid, a plant hormone vital for signaling during the wound response (Peebles et al., 2009).

In various resin-producing plants, one activity that intentionally causes wounds in plant tissues is the tapping of sap. The impact of tapping on the trunk of the frankincense tree, performed by humans, is primarily observed in the amount of IAA produced by the isolated endophytic bacteria and their capacity to generate IAA. Tapping with frankincense sap influences IAA production by endophytic bacteria (Susilowati et al., 2025).

Certain endophytic bacteria that reside within plant tissues produce indole acetic acid (IAA), which can influence the physiological responses of plants to wounding. Recent studies have identified various endophytic bacterial strains, such as *Bacillus cereus* and *Pseudomonas putida*, capable of synthesizing IAA through different biosynthetic pathways, including the indole-3-acetamide (IAM) and tryptamine (TAM) pathways. These bacteria use plant-derived intermediates to produce IAA, thereby modulating plant growth and stress responses (Feng et al., 2024). Endophytic bacteria that produce IAA play essential roles in plant wound responses by facilitating tissue regeneration and stress reduction. In response to injury, plants release signaling molecules, including tryptophan, which serves as a precursor for IAA biosynthesis by these microbes. Increased IAA production by endophytes promotes cell division, stimulates callus formation, and aids in vascular tissue repair at the wound site. This mutualistic relationship enables plants to recover more effectively from mechanical damage and pathogen attacks (Spaepen et al., 2007; Dittmann et al., 2015).

The symbiotic adaptation of endophytic bacteria to wounding stress has been demonstrated to have various effects on host plants, including phytohormone signaling and plant defense responses. The presence of endophytic bacteria can escalate the adaptation of plants to biotic or

Fig. 4: Phylogenetic tree of bacterial isolate S4 based on 16s rRNA sequences using the neighbor-joining method, bootstrap 1000x.

abiotic stresses such as drought, salt, nutritional deficiency, heavy metal stress, and temperature (Ameen et al., 2024). Susilowati et al. (2025) reported the ability of endophytic bacterial isolates from tapped frankincense trees. Tapping with frankincense sap may influence the ability of endophytic bacteria to produce IAAs.

Statistical analysis revealed that IAA production by endophytic bacteria in tapped trees differed significantly from that in untapped trees. Consequently, tapping considerably impacted IAA production in *S. paralleloneurus* trees.

The analysis demonstrated that only 7 bacterial species from the untapped stems survived morphological characterization, whereas 16 species were identified in the tapped stems. This suggests that human activities have a significant impact on environmental microbiomes.

The highest IAA concentration was observed in isolate S4, reaching 26.75ppm, whereas the lowest concentration was detected in isolate TS5 (0.04ppm. The intensity of the red color directly correlated with IAA production. This relationship is due to the more efficient utilization of tryptophan by these bacteria, as tryptophan serves as a precursor in the metabolic pathway for synthesizing amino acids, including IAA. The production of IAA by bacteria from tapped trees was inversely related to IAA production by bacteria from untapped trees. This variation is believed to be influenced by human activity, which tends to occur more often in the tapped trees.

Damage to plant tissues triggers auxin production. This indicated that endophytic bacteria capable of synthesizing IAA may influence the overall response of plants to physical injury. A key component of this response is the increased synthesis and accumulation of auxins, which serve as crucial regulators of various defense mechanisms that follow (Meng et al., 2019). Auxin is widely recognized as a critical factor in controlling various plant physiological processes, such as growth, development, and stress responses (Meng et al., 2019). In cases of tissue damage, auxin functions as a vital signaling molecule that triggers multiple defense-related pathways (Kunkel and Harper, 2018). Studies have demonstrated that *Bacillus* species, a type of bacterium recognized for their IAA production, can trigger systemic resistance in plants, potentially improving their ability to withstand abiotic stress (Dimkpa et al., 2009). Furthermore, endophytic bacteria with growth-promoting properties, isolated from *Ophioglossum reticulatum* L., have been shown to produce IAA, solubilize calcium phosphate, and generate siderophores, indicating their potential role in enhancing plant physiology and resilience (You et al., 2010). The endophytic strain Bacillus subtilis 26D Increases IAA levels and promotes potato (Sorokan et al., 2021).

Kocuria palustris is usually found in humid environments such as swamps or humid soil, which are natural habitats for these bacteria. *Kocuria palustris* has a coccus (spherical) shape and is a bacterium. Several studies have successfully isolated the genus Kocuria from various sources, such as agricultural soil, contaminated soil, marine sediment, fresh water, waste, clinical samples, rhizosphere, and plant endosphere (Zacaria Vital et al., 2019).

K. palustris is not commonly associated with human skin; however, it belongs to the genus gram-positive Kocuria, which includes species recognized as normal components of the skin microbiota (Kandi et al., 2016; Ziogou et al., 2023). The literature suggests that *K. palustris* exhibits fungicidal activity, making it a promising biocontrol agent and plant biostimulant. Recent studies have highlighted the potential of *K. palustris* as a biocontrol agent and plant biostimulant owing to its fungicidal activity. For example, a culture extract of *K. palustris* 19C38A1 demonstrated significant antifungal effects against *Fusarium oxysporum*, a pathogen responsible for vascular wilt in various crops (Setiawan et al., 2022).

Although traditionally considered nonpathogenic, *K. palustris* has emerged as an opportunistic pathogen,

particularly in immunocompromised individuals. Case reports have documented instances of *K. palustris* bacteremia in patients undergoing chemotherapy or hemodialysis. Additionally, *K. palustris* has been implicated in ocular infections such as ulcerative keratitis, especially in patients with underlying conditions such as vitamin A deficiency (Mattern & Ding, 2014; Varghese et al., 2023; Ziogou et al., 2023).

To date, no scientific report has specifically confirmed that *K. palustris* produces IAA, an auxin hormone that is essential for plant growth. However, studies indicate that other species within the genus *Kocuria*, such as *Kocuria rosea*, possess this ability. In research conducted by Karnwal (2019), *K. rosea* VB1, isolated from industrial wastewater, exhibited significant IAA production when cultured with L-tryptophan, reaching concentrations of 123.7 ng/ml at a L-tryptophan concentration of 500 µg/ml. Furthermore, IAA production increased when the bacteria were cultured alongside corn root exudates, indicating that interactions with plants can enhance IAA biosynthesis.

The biosynthesis of IAA in bacteria generally relies on metabolic pathways that utilize l-tryptophan as a precursor. Some recognized pathways include indole-3-pyruvate (IPA), indole-3-acetamide (IAM) and tryptamine (TAM) (Spaepen et al., 2007; Duca et al., 2014). However, to date, no specific studies have been conducted to identify the IAA biosynthetic pathway in *K. palustris*. Given that other species within the *Kocuria* genus can produce IAA, it is plausible that *K. palustris* possesses similar capabilities. Additional research is required to confirm this potential and to clarify the associated biosynthetic mechanisms.

These findings underscore the ecological versatility of *K. palustris*, which ranges from environmental inhabitants and agricultural allies to opportunistic human pathogens. Its adaptability to diverse environments and interactions with various hosts highlights the need for further research on its potential applications and implications for human health.

Conclusion

Endophytic bacteria from tapped frankincense trees showed a significantly higher production of indole-3-acetic acid (IAA) than those from untapped trees, with isolate S4 producing the highest levels. Molecular analysis identified *K. palustris* as the primary IAA producer, highlighting its potential for enhancing plant growth and resilience. The tapping process is known to increase IAA production by these bacteria; however, this study did not examine their agricultural applications. IAA-producing bacteria are commonly used as biostimulants, but further research is needed to explore their effects on plant development.

DECLARATIONS

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Conflict of Interest: The author declares that there is no conflict of interest regarding the publication of this manuscript. In addition, the authors have fully addressed the ethical issues, including plagiarism, informed consent, misconduct, data fabrication and/or falsification, double publication and/or submission, and redundancy.

Data Availability: All relevant data are included within the article.

Ethics Statement: This study did not require ethical review, as it did not involve sensitive human data or animal subjects.

Author's Contribution: AS and MC: conceptualization, field sampling, and writing original draft and revised; FO: laboratory research performed, and data analysis; ATP and RS: data analysis and writing original draft; YK: visualization and figure preparation, manuscript editing; SHL: editing manuscript, and review.

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