



Research article

Characterization of indole-3-acetic acid-producing marine yeasts and their effect on tomato (*Solanum lycopersicum* L.) seedlings

Chutima Kaewkrajay^{a,*}, Tuankumari Kotabaru^a, Tida Dethoup^b

^a Division of Microbiology, Faculty of Science and Technology, Phranakhon Si Ayutthaya Rajabhat University, Phra Nakhon Si Ayutthaya 13000, Thailand

^b Department of Plant Pathology, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand

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Abstract

Importance of the work: The marine yeasts *Rhodotorula mucilaginosa* DMKU 7233-1 and *Papiliotrema laurentii* DMKUFC10-4 had strong potential for producing indole-3-acetic acid (IAA). Their cell suspension promoted tomato seed germination and increased stem size.

Objectives: To screen IAA-producing yeasts, analyze their phytobeneficial attributes, evaluate their antagonistic activity against *Agroathelia rolfsii*, to study low-cost substrates suitable for IAA production and to evaluate the effectiveness of yeast cells on tomato seed germination.

Materials and Methods: In total, 49 marine yeasts were screened for IAA production. Phytobeneficial attributes (nutrient solubilization, production of cell wall-degrading enzymes and synthesis of active substances) were evaluated. The antagonistic activity was studied between the yeasts and *A. rolfsii*. Low-cost carbon sources for IAA production were investigated and tomato seed bioassays were conducted.

Results: The marine yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 produced the best results for IAA production. Although neither strain could solubilize phosphate or zinc oxide, and they did not produce siderophores or NH_3 , both strains were able to produce catalase and cellulase. There was no antagonistic activity between either of the yeast strains and *A. rolfsii*. IAA production in sugarcane molasses medium amended with 0.1% L-tryptophan (L-trp) yielded the best results at $1,379.4 \pm 29.6$ mg/L with DMKU 7233-1 and 681.4 ± 38.8 mg/L with DMKUFC10-4. Tomato seedlings treated with *P. laurentii* DMKUFC10-4 had a high germination rate (100%), while *R. mucilaginosa* DMKU 7233-1 produced the best outcome based on enhancement of stem size.

Main finding: The yeast strains DMKU 7233-1 and DMKUFC10-4 were effective at producing IAA in a medium amended with 0.1% L-trp. Sugarcane molasses was a suitable carbon source. Cell suspension of both yeast strains promoted the growth of tomato seedlings.

* Corresponding author.

E-mail address: kchutima@aru.ac.th (C. Kaewkrajay)

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Introduction

Indole-3-acetic acid (IAA) is the most common auxin-class phytohormone generated by plants and plays a major role in various aspects of plant growth such as cell elongation, cell differentiation, root initiation and development, embryo development, phototropism and geotropism (Zhao, 2010; Chandra et al., 2018). Additionally, following the plant's assimilation of nutrients from the soil, IAA improves the length, branches, hairs and laterals of the roots (Datta and Basu, 2000). Therefore, IAA is an important plant growth promoter that is often considered superior to other growth-promoting factors such as phosphate solubilization and siderophore production (Etesami et al., 2015). IAA is produced not only by plants, but also by microorganisms such as bacteria, fungi and yeasts (Tudzynski and Sharon, 2001; Tsavkelova et al., 2006). Microbial-derived IAA effects are similar to those derived from plants (Sun et al., 2014). Among the aforementioned microorganisms, various yeast species can stimulate plant growth through the production of compounds that resemble plant hormones (Nassar et al., 2005).

Yeasts are unicellular fungi that are found in various habitats, including marine environments, with these yeasts having a strong ability to live in extreme environments, suggesting a unique capacity for the synthesis of functional biomolecules with potential applications in agricultural, chemical, cosmetic, food and pharmaceutical industries (Chi et al., 2016; Sarkar and Rao, 2016). Marine yeasts have shown promise in agricultural applications (Lara-Capistran et al., 2020; Kaewkrajay and Dethoup, 2024). However, research is scarce on using marine yeasts as growth-promoting agents. Nimsi et al. (2023) reviewed marine isolates and reported that *Rhodotorula* was a major plant growth-promoting yeast, followed by *Kazhakistania* and *Rhodosporidium*. Additionally, IAA-producing marine yeast species have been isolated, including *Candida orthopsilosis* and *Rhodotorula mucilaginosa* from Red Sea water (Abdel-Kareem et al., 2021), *Candida tropicalis* and *Aureobasidium melanogenum* from mangroves (Nimsi et al., 2024) and *Debaryomyces hansenii* and *Papiliotrema laurentii* from marine environment (Lara-Capistran et al., 2020). Therefore, a study of the isolation, identification and characterization of IAA-producing yeasts should be of great value for agricultural applications.

Tomato (*Solanum lycopersicum* L.) is a suitable source of phytochemicals and nutrients such as folate, iron, lycopene, potassium and vitamin C (Toor et al., 2005; Bhowmik et al., 2012).

According to updated data from the FAO, 189.1 million t of tomatoes were produced worldwide in 2021, representing a 2% increase from the 184.8 million t produced in 2020 and a 4% increase from the 2018–2020 average of 182.7 million t (Branthôme, 2023). Tomatoes are grown in many countries, including Thailand (Charoenvilaisiri et al., 2020). Besides water-soluble fertilizer such as phosphorus, IAA affects tomato seedlings, where its transport has been thoroughly studied (Hughes, 2023). Additionally, a major problem is the severe damage to tomato plant seedlings caused by *Agroathelia rolfsii* (Syn: *Sclerotium rolfsii*); this pathogen is widely distributed in tropical and subtropical regions and is well known as a soil-borne fungus, being recognized as an omnipathogenic parasite capable of infecting more than 500 plant species worldwide—particularly important economic crops such as chili pepper (*Capsicum annuum* L.; Boukaew et al., 2025), sugar beet (*Beta vulgaris* L.; Farhaoui et al., 2024) and tomato (*Solanum lycopersicum* L.; Coulibalya et al., 2022). Therefore, the aims of the current research were: 1) to screen marine yeasts that produce IAA; 2) to analyze the phytobeneficial attributes and evaluate antagonistic activity against *A. rolfsii*; 3) to study low-cost substrates suitable for IAA production; and 4) to evaluate the effectiveness of yeast cell suspension on tomato seed germination.

Materials and Methods

Microorganisms

Primary screening for IAA production was carried out using a collection of 49 marine yeasts (isolated from seawater, sea sediments, seaweed and marine invertebrates) identified by Kaewkrajay et al. (2020, 2021). These yeasts were stored in the Microbiology Laboratory at Phranakhon Si Ayutthaya Rajabhat University, Thailand. All the yeasts were stored in yeast extract-malt extract (YM) broth (3 g/L yeast extract, 3 g/L malt extract, 5 g/L peptone and 10 g/L glucose), supplemented with 10% (volume per volume) glycerol and maintained at -80°C. Before the study, these yeasts were reactivated by culturing on YM agar medium prepared with artificial seawater, containing the following components dissolved in 1 L of reverse osmosis (RO) water: NaCl 23.5 g, MgCl₂·6H₂O 5.0 g, Na₂SO₄ 3.9 g, CaCl₂ 1.1 g, KCl 0.66 g, NaHCO₃ 0.2 g, KBr 0.1 g, H₃BO₃ 0.026 g, SrCl₂·6H₂O 0.024 g and NaF 0.003 g. The pH was adjusted to 7.8–8.2 using a sodium carbonate solution (Indian Standard, 1978). The cultures were incubated at 25°C before storage on slants of YM agar at 4°C.

The pathogen (*A. rolfsii*) was obtained from the Department of Plant Pathology, Faculty of Agriculture, Kasetsart University, Bangkok, Thailand. It had been isolated from diseased cucumber seedlings. The sclerotial growth on the diseased cucumber seedlings was placed on potato dextrose agar (PDA) and incubated for 3 d. The fungal mycelia that emerged from a sclerotium were collected and cultured on PDA plates, followed by identification based on the morphological characteristics of the mycelia and sclerotia observed on the PDA plates.

In vitro screening of indole-3-acetic acid production

Assessment of IAA production was performed by transferring a loopful of active yeast that had been cultured on yeast extract peptone dextrose (YPD) agar slant (10 g/L yeast extract, 20 g/L peptone, 20 g/L glucose and 20 g/L agar) at 30°C for 24 hr into 50 mL of YPD broth in a 250 mL Erlenmeyer flask. Each flask was incubated on a rotary shaker (NB-205VL; N-Biotek; Gyeonggi-do, Korea) with a shaking speed of 160 revolutions per minute (rpm) at 30°C for 24 hr. The inocula volume was calculated to give an initial cell concentration corresponding to an optical density (OD) at 600 nm of 1.0, before being introduced to 100 mL YPD broth samples either with or without 0.1% L-trp. Then, the culture flasks were placed on a rotary shaker at 160 rpm and 30°C. After 7 d, each culture was collected for biomass measurement and IAA production analysis.

Phosphate and zinc oxide solubilization assay

The phosphate and zinc oxide solubility levels of the selected IAA-producing yeasts were evaluated following the method described by Rokhbakhsh-Zamin et al. (2011), with slight modification. The phosphate solubility was performed by spotting 5 μ L of each yeast cell suspension (1×10^8 cells/mL) onto the surface of a modified Pikovskaya's agar plate medium containing 5 g/L $\text{Ca}_3(\text{PO}_4)_2$, 10 g/L glucose, 0.5 g/L $(\text{NH}_4)_2\text{SO}_4$, 0.1 g/L $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.2 g/L KCl, 0.5 g/L yeast extract and 20 g/L agar. Each plate was incubated at 25°C for 5 d. The existence of a clear zone surrounding the yeast colonies indicated a positive result. On the other hand, zinc oxide solubility was assessed by triplicated-spotting 5 μ L of a 1×10^8 cells/mL yeast culture onto agar plate medium containing 12 g/L ZnO, 10 g/L glucose, 0.5 g/L $(\text{NH}_4)_2\text{SO}_4$, 0.1 g/L $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.2 g/L KCl, 0.5 g/L yeast extract and 20 g/L agar. After 5 d of incubation at 25°C, the clear zone on culture plates was measured.

Siderophore production

Chrome azurol S (CAS) agar was used to evaluate the production of siderophores, based on Schwyn and Neilands (1987). Briefly, 0.0605 g of CAS was weighed and dissolved in 50 mL of distilled water, then mixed with 10 mL of FeCl_3 solution, which was prepared by dissolving 0.0027 g of $\text{FeCl}_3 \cdot 6\text{H}_2\text{O}$ in 10 mL of 10 mM HCl. Under gentle stirring, 0.0729 g of cetyltrimethyl ammonium bromide in 40 mL of distilled water was gradually poured into the mixture. The resulting, blue-colored solution was sterilized by autoclaving at 121°C for 15 min. Then, the dye solution was mixed with sterile YPD medium at a ratio of 10:90 and poured into a sterile Petri dish (90 mm diameter). Then, 5 μ L of a 1×10^8 cell/mL yeast culture were spotted onto the CAS agar plates. Each plate was incubated at 25°C for 7 d. When the blue color turned orange, it was considered that yeasts had produced siderophores. Subsequently, the width of the orange zone formed around each yeast colony was measured and recorded.

Catalase test

The catalase test was performed by spotting 5 μ L of a 1×10^8 cell/mL yeast culture onto YM agar plates. Prior to autoclaving, the YM agar was adjusted to an initial pH 6.8. The culture was incubated at 25°C. After 3 d, 3% hydrogen peroxide (50 μ L) was added directly to the yeast colonies. Oxygen bubbles were indicative of a positive result (Fernandez-San Millan et al., 2020).

Ammonium production

A sample of 5 mL of peptone water (10.0 g/L peptone and 5.0 g/L NaCl; pH 6.8) was prepared in a test tube. Then, 100 μ L of yeast cell suspension (1×10^8 cells/mL) was added and placed on a rotary shaker with a shaking speed of 160 rpm at 25°C. After 5 d, the sample was collected by centrifuging the culture at 4,000 rpm for 5 min. A 1 mL of aliquot was mixed with 100 μ L of Nessler's reagent. A color change from yellow to brown signified the production of NH_3 (Cappuccino and Sherman, 2002).

Extracellular lytic enzyme activities

The activities of lytic enzymes (cellulase, chitinase and protease) were assessed to identify enzymes that could protect plants against phytopathogens. Cellulase activity

was determined by spotting 5 μ L of a yeast culture (1×10^8 cells/mL) on the medium agar plate containing 4.0 g/L of carboxymethylcellulose (CMC) as a substrate and incubating at 25°C. After 7 d, staining was performed using Lugol's iodine solution. A positive result was indicated by the appearance of a clear halo around a yeast colony (Kasana et al., 2008). Chitinase activity was determined by spotting each sample on YPD media containing 12 g/L of colloidal chitin. After 3 d of incubation at 25°C, the plates were flooded with 0.1% Congo Red solution. The appearance of a clear halo around the colonies indicated a positive result (Souza et al., 2009). Furthermore, each sample was spotted on YM agar plates amended with 10% skim milk to determine the protease activity. Each plate was kept at 25°C for 5 d. A positive result indicated by a light halo around a yeast colony (Gardini et al., 2006). Yeast colonies and halo zone diameters were measured. Degradation activity was calculated using the formula (Colony diameter + Halo zone diameter) / Colony diameter (Fernandez-San Millan et al., 2020).

Antagonistic activity against A. rolfsii

Antagonistic activity of IAA-producing yeasts against *A. rolfsii* was assessed using a confrontation assay. Yeasts were cultured on YM plates and molds on PDA plates, then incubated at 30°C for 24 hr and 72 hr, respectively. Active yeast cells were inoculated by streaking linearly 4 cm on a PDA plate (starting 2 cm from one edge) and then were incubated at 30°C. After 2 d, the mycelial plugs of fungal pathogen were pierced using a 5 mm sterile steel borer and then placed 5 cm apart from the yeast strip. The plates were incubated at 30°C for 3 d. PDA plates inoculated with the only the fungal pathogen served as controls. The decrease in radial mycelial growth relative to the control was calculated according to the Equation 1:

$$\% \text{ Inhibition} = [(C - T) / C] \times 100 \quad (1)$$

where C is the radial mycelial growth of pathogen in the control and T is the radial mycelial growth of the pathogen in the confrontation assay.

The experiments were conducted in triplicate. Yeast strains capable of inhibiting *A. rolfsii* were stored at 4°C for future research.

Indole-3-acetic acid production in low-cost substrate media

The IAA-producing yeasts were cultivated in a medium containing cassava starch hydrolysate, distillery slops and

sugarcane molasses amended with 0.1% L-trp. Cassava starch hydrolysate was prepared according to the method described by Kaewkrajay et al. (2014). Briefly, soil and sand were removed from the cassava rhizomes before peeling and chopping. Then, the moist chips were dried in the sun for 2 d and blended using an electrical blender. The resulting flour was sieved through a 100-mesh screen. Then saccharification of cassava starch was performed by dissolving 30% cassava flour in distilled water and adjusting to an initial pH of 6.0. Industrial grade α -amylase (Sinobios; Shanghai, China; 4,000 U/g) was added for liquefaction at a concentration of 1 g per kg of dry starch. The temperature was maintained at between 95°C and 100°C for 2 hr with vigorous agitation. Then, CaCl_2 was added at a concentration of 1 g per kg of dry starch to the slurry for enzyme stabilization. After 2 hr, the temperature of the fluid dextrin was reduced to 65°C and the pH was adjusted to 4.0 using 1 M HCl. Amyloglucosidase (Sigma; St. Louis, Missouri, USA; 1,000 U/g) at a concentration of 0.45 g per kg of dry starch was loaded to complete saccharification. The solution was incubated at 65°C for 24 hr under agitation in a water bath shaker. After the saccharification had been completed, the reaction was stopped by boiling for 20 min. The dinitro salicylic acid (DNS) method was used to analyze the concentration of reducing sugar.

To prepare the inoculum, a loopful of active yeast cells was transferred to 50 mL of YM broth and incubated on a rotary shaker at 160 rpm and 30°C for 24 hr. The inoculum volume was pre-calculated before transferring into 100 mL of medium broth in 250 mL Erlenmeyer flasks, to achieve an initial cell concentration with an OD at 600 nm of 1.0. The medium broth consisted of cassava starch hydrolysate, distillery slops, or sugarcane molasses as a reducing sugar at a concentration of 20 g/L, along with 0.5 g/L NH_4Cl , 1 g/L L-trp, with the initial pH adjusted to 6.0. Then, cultivation was performed on a rotary shaker at 160 rpm and 30°C for 7 d. The yeast cells were harvested to analyze the biomass and IAA concentration. The experiments were conducted in triplicate.

Tomato seed bioassay

Tomato seeds were surface sterilized with 1% sodium hypochlorite for 30 min and then rinsed five times with sterile RO water, before placing on a sterile filter paper to dry.

Marine yeast was cultivated on a YPD agar slant for 24 hr at 30°C. The yeast cell suspension was prepared by transferring a loopful of active yeast cells into 100 mL of YPD broth amended with 0.1% L-trp in a 250 mL Erlenmeyer flask,

followed by incubation on a rotary shaker at 160 rpm and 30°C for 48 hr. After incubation, the entire yeast culture was transferred to a sterile 50 mL conical centrifuge tube and centrifuged at 4,000 rpm for 5 min. The resulting cell pellets were washed twice with sterile RO water and resuspended in sterile RO water under aseptic conditions. Then, the cell suspension was diluted to a density of 1×10^8 cells/mL with RO water. Next, 5 mL of each 1×10^8 cells/mL yeast culture was poured onto plates over the tomato seeds. Each plate contained 20 tomato seeds. The negative control used 5 mL of water instead of yeast culture, while the positive control used 2.5 mg/L commercial IAA (SRL; Sisco Research Laboratories Pvt. Ltd.; Mumbai, India) was utilized. Seeds were incubated in a growth cabinet (Sanyo; Ueda, Japan) at 25°C for 7 d with a relative humidity of 60%. The germination was recorded daily for 7 d. Six treatments were designed: T1, 20 tomato seeds + 5 mL distilled water (negative control); T2, 20 tomato seeds + 5 mL commercial IAA (positive control); T3, 20 tomato seeds + 5 mL of *R. mucilaginosa* DMKU 7233-1 yeast cell suspension; T4, 20 tomato seeds + 5 mL of *P. laurentii* DMKUFC10-4 yeast cell suspension; T5 and T6: 20 tomato seeds + 5 mL cell-free filtrates of selected yeast isolates.

Analytical methods

The dry cell weight was determined by sampling 5 ml of yeast culture, which was centrifuged at 4,000 rpm for 10 min. After two washes with sterile RO water, the cell pellets were resuspended in 0.5 mL of RO water and placed in an aluminum foil cup. The cell pellets in each aluminum foil cup were dried in a hot-air oven at 65°C until constant weight, based on analytical balance readings.

The IAA concentration was analyzed by vigorously mixing of 1 mL of sample and 1 mL of Salkowski's reagent (49 mL of 35% perchloric acid and 1 mL of 0.5 M $\text{FeCl}_3 \cdot 6\text{H}_2\text{O}$) and leaving the mixture to stand at room temperature for 30 min (Gordon and Weber, 1951). Each sample was measured in triplicate at a wavelength of 540 nm. The IAA concentration of each sample was estimated by comparing it with a standard curve. The standard curve was plotted in the range 0–100 µg/mL using commercial IAA.

Reducing sugar was analyzed using the DNS method (Miller, 1959). High-reducing sugar concentrations were diluted using distilled water until the absorbance at 540 nm wavelength was in the range 0.1–1.0. Sugar concentration was determined by a comparison with the glucose standard curve.

Statistical analysis

Data were expressed as mean $\pm$ SD. Significant differences among treatments were determined using one-way analysis of variance (ANOVA), followed by Duncan's multiple range post hoc test ($p < 0.05$), using SPSS Statistics for Windows (version 21; IBM Corp.; Armonk, NY, USA).

Results

Screening of indole-3-acetic acid-producing yeast

Out of the 49 tested marine yeasts, 10 had high IAA production when cultivated in YPD broth with and without L-trp at a shaking speed of 160 rpm and 30°C for 7 d. Among these yeast strains, DMKU 7233-1 cultivated in a medium with and without L-trp produced IAA at higher concentrations than for the other stains, followed by DMKUFC10-4 (Table 1).

Table 1 High indole-3-acetic acid (IAA)-producing yeasts in YPD broth with and without L-trp.

Yeast species	DDBJ Accession number	IAA production (mg/L)	
		without L-trp	with 0.1% L-trp
<i>Candida orthopsilosis</i> DMKUJC47-2	LC529389	51.18 $\pm$ 0.76 ^b	78.18 $\pm$ 2.77 ^c
<i>Naganishia liquefaciens</i> DMKU3222-2	LC511617	53.03 $\pm$ 2.89 ^b	77.39 $\pm$ 1.19 ^c
<i>Papiliotrema laurentii</i> DMKUFC10-4	LC529403	63.55 $\pm$ 0.15 ^a	210.92 $\pm$ 1.00 ^b
<i>Papiliotrema laurentii</i> DMKU JC12-1	LC431014	54.74 $\pm$ 0.30 ^b	98.86 $\pm$ 2.76 ^d
<i>Rhodotorula mucilaginosa</i> DMKU 329-1	LC415315	55.00 $\pm$ 2.13 ^b	155.63 $\pm$ 5.41 ^c
<i>Rhodotorula mucilaginosa</i> DMKUC3213-2	LC415317	55.13 $\pm$ 2.89 ^b	164.75 $\pm$ 4.87 ^c
<i>Rhodotorula mucilaginosa</i> DMKU 729-1	LC430111	53.82 $\pm$ 1.98 ^b	165.53 $\pm$ 2.04 ^c
<i>Rhodotorula mucilaginosa</i> DMKU 7233-1	LC430585	66.97 $\pm$ 0.46 ^a	260.43 $\pm$ 3.37 ^a
<i>Saccharomyces cerevisiae</i> DMKU4A-2	LC497826	53.55 $\pm$ 5.32 ^b	96.61 $\pm$ 1.75 ^d
<i>Saccharomyces cerevisiae</i> DMKU12M-1	LC497466	51.45 $\pm$ 2.58 ^b	93.47 $\pm$ 2.99 ^d

DDBJ = DNA Data Bank of Japan.

Mean $\pm$ SD within each column followed by different lowercase superscript letters indicate significant differences ($p < 0.05$).

Additionally, IAA from these yeasts produced a high amount of IAA when cultivated in a medium supplemented with 0.1% L-tryptophan. Based on the similarity of the D1/D2 domain sequences of the LSU rRNA gene, three strains belonged to two known yeast species within the phylum Ascomycota, namely *Candida orthopsilosis* and *Saccharomyces cerevisiae*. Another seven strains belonged to three known yeast species within the phylum Basidiomycota, namely *Naganishia liquefaciens*, *Papiliotrema laurentii* and *Rhodotorula mucilaginosa*. Among these 10 strains, the yeast producing the highest level of IAA was *R. mucilaginosa* (four strains), followed by *P. laurentii* (two strains) and *S. cerevisiae* (two strains).

As both *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 had high IAA production, they were selected for further studies.

Siderophore production, phosphate solubilization and zinc oxide solubilization

Siderophores are small molecules that are produced and secreted by microorganisms to mediate the uptake of essential Fe^{3+} into cells (Raines et al., 2015). Siderophores can limit the availability of iron needed for pathogen growth; hence they are important for promoting plant health (Ahmed and Holmström 2014). The current study used CAS medium agar plates to determine siderophore production, where the presence of siderophores was indicated by a blue-to-orange color change. The yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 did not produce siderophores (Fig. 1).

Phosphate is a macronutrient required by plants for growth and development; however, its availability can be

limited by chemical fixation in the soil with other metal cations (Johan et al. 2021). In the current study, there was no phosphate-solubilizing activity displayed by the marine yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 during the *in vitro* assay.

Zinc oxide solubilizing activity was assessed using a medium containing 12 g/L ZnO. No clear zone appeared around either of the marine yeast colonies *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4.

NH_3 production and catalase test

No yellow-to-brown color was observed after adding 100 μL of Nessler's reagent to 1 mL of yeast cell-free supernatant, indicating that the marine yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 could not produce NH_3 .

The catalase enzyme catalyzes the breakdown of hydrogen peroxide (H_2O_2) to water (H_2O), which is important for microorganisms to resist injury (Kaushal et al. 2018; Freimoser et al., 2019). In the current study, both yeast strains produced oxygen (Fig 1).

Cell wall-degrading enzyme production

The yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 were able to hydrolyze CMC, indicating that they produced cellulase enzymes, which may help protect plants against fungal pathogens. Furthermore, *R. mucilaginosa* DMKU 7233-1 had positive protease activity, while *P. laurentii* DMKUFC10-4 did not. However, neither strain had chitinase activity (Fig. 2; Table 2).

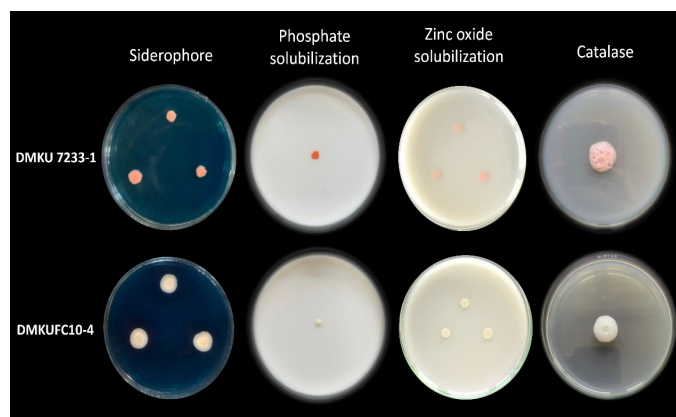


Fig. 1 Evaluation of siderophore production, phosphate solubilization, zinc oxide solubilization and catalase enzyme activity in marine yeasts *Rhodotorula mucilaginosa* DMKU 7233-1 and *Papiliotrema laurentii* DMKUFC10-4.

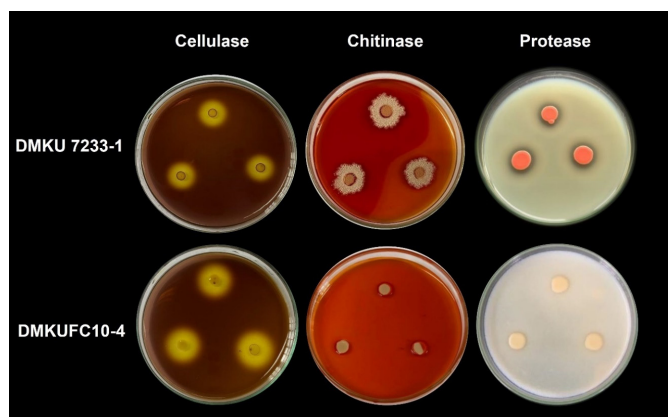


Fig. 2 Cell wall-degrading enzyme assay for cellulase, chitinase and proteinase in marine yeasts *Rhodotorula mucilaginosa* DMKU 7233-1 and *Papiliotrema laurentii* DMKUFC10-4

Table 2 Degradation activity of cell wall-degrading enzymes from marine yeasts (*Rhodotorula mucilaginosa* and *Papiliotrema laurentii*).

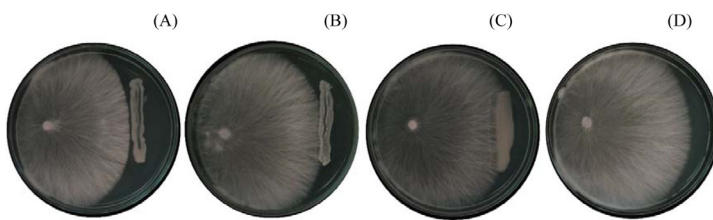
Yeast strain	Cellulase (DA)	Chitinase (DA)	Protease (DA)
<i>R. mucilaginosa</i> DMKU 7233-1	1.91±0.03	0	1.16±0.02
<i>P. laurentii</i> DMKUFC10-4	3.22±0.12	0	0

DA = degradation activity (Colony diameter + Halo zone diameter) / Colony diameter.

Values presented as mean ± SD.

Antagonistic activity

The evaluation of antagonistic activity between IAA-producing yeasts and *A. rolfsii* using confrontation assay revealed that 3 out of 10 yeast strains, namely, *S. cerevisiae* DMKU4A-2, *C. orthopsilosis* DMKUJC47-2 and *P. laurentii* DMKU JC12-1, slightly inhibited the mycelial growth of *A. rolfsii* (Fig. 3) at 13.7±7.7%, 9.2±4.1% and 7.7±0.8%, respectively. Furthermore, the strains *R. mucilaginosa* DMKU 7233-1, *P. laurentii* DMKUFC10-4 and the remaining strains did not inhibit *A. rolfsii*.

**Fig. 3** Antagonistic activities of marine yeasts against *Agroathelia rolfsii*: (A) *Saccharomyces cerevisiae* DMKU4A-2; (B) *Candida orthopsilosis* DMKUJC47-2; (C) *Papiliotrema laurentii* DMKU JC12-1; and (D) *A. rolfsii* alone as the control. Plates were incubated on potato dextrose agar at 30°C for 3 d.

Indole-3-acetic acid production in low-cost carbon sources

The yeast strains *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 produced the most IAA using tryptophan-supplemented and tryptophan-free media. Given the role of tryptophan as a primary precursor during IAA synthesis, supplementation with tryptophan in a culture medium could be expected to lead to superior IAA production (Pedraza et al. 2004). In the current study, both yeast strains produced high levels of IAA in the sugarcane molasses medium amended with 0.1% L-trp. The highest IAA concentrations were produced by the yeast strains *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4: 1,379.4±29.6 mg/L and 681.4±38.8 mg/L, respectively. Furthermore, the IAA content was the highest in the medium containing sugarcane molasses for *R. mucilaginosa* DMKU 7233-1 and distillery slops for *P. laurentii* DMKUFC10-4 (Table 3).

Assessment of seedling growth promotion on plates

Tomato seeds were treated with the marine yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 and compared to water (negative control) and commercial IAA (positive control). Germination was considered successful when the tomato radicle length exceeded 2 mm. No seed germination occurred on day 1. Seed germination started on day 2 when the tomato seeds were treated with water, commercial IAA and a suspension of yeast cell strains DMKU 7233-1 and DMKUFC10-4. The best tomato seed germination occurred for the water, commercial IAA and yeast cell suspension of strain DMKUFC10-4 treatments (100 ± 0.0% for 4–6 d), followed by the treatment of the yeast cell suspension of strain DMKU 7233-1 (98.3 ± 2.6% for 4 d). Seed germination was not observed for the remaining treatments (Fig. 4A, Table 4).

Table 3 Indole-3-acetic acid (IAA) concentration and content for marine yeasts (*Rhodotorula mucilaginosa* and *Papiliotrema laurentii*) in various carbon sources with 0.1% L-trp.

Yeast species	Carbon source	IAA concentration (mg/L)	IAA content (mg/g dry weight)
<i>R. mucilaginosa</i> DMKU 7233-1	Cassava starch hydrolysate	38.1±0.9 ^c	11.5±0.3 ^c
	Distillery slops	813.7±4.6 ^b	180.8±1.0 ^b
	Sugarcane molasses	1,379.4±29.6 ^a	205.9±4.4 ^a
<i>P. laurentii</i> DMKUFC10-4	Cassava starch hydrolysate	51.4±1.2 ^c	11.2±0.3 ^c
	Distillery slops	568.6±8.5 ^b	123.6±1.8 ^a
	Sugarcane molasses	681.4±38.8 ^a	94.6±5.4 ^b

Mean ± SD values followed by different lowercase superscript letters indicate significant difference ($p < 0.05$) in IAA concentrations and contents for each carbon source within each yeast species.

The mean radical length was significantly greater in the water treatment (67.8 ± 2.6 mm) than in any of the other treatments after 7 d, followed by the commercial IAA treatment (30.1 ± 2.1 mm). There was no significant difference in tomato root length for the seeds treated with *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 yeast cells (Fig. 4B; Table 4). Although the root length was the longest in the water treatment,

this treatment did not appear to cause lateral root development. Furthermore, some lateral roots appeared in tomato seeds treated with commercial IAA and cell suspensions of *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 (Fig. 4C).

The shoot length was significantly greater in seedlings treated with water (67.1 ± 1.7 mm) than in seedlings treated with commercial IAA (54.3 ± 1.0 mm) and cell suspensions of *P. laurentii* DMKUFC10-4 (42.4 ± 0.7 mm). However, the stem diameter of water-treated tomatoes was small compared to that of tomatoes treated with IAA from *R. mucilaginosa* DMKU 7233-1 cell suspension (Fig. 4B; Table 4).

Discussion

Increasing concerns about human health, food safety and environmental problems have led to an increasing demand for biofertilizers (Kumar et al., 2022). In the current study, 10 strains from 5 known yeast species, namely *C. orthopsilosis* (DMKUJC47-2), *N. liquefaciens* (DMKU3222-2), *P. laurentii* (DMKUFC10-4 and DMKU JC12-1), *R. mucilaginosa* (DMKU 329-1, DMKU C3213-2, DMKU 729-1 and DMKU 7233-1) and *S. cerevisiae* (DMKU4A-2 and DMKU12M-1), were identified as IAA producers.

In the YPD medium without L-trp, the yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 produced 66.97 ± 0.46 mg/L and 63.55 ± 0.15 mg/L IAA, respectively. Furthermore, the production of IAA significantly increased, peaking at 260.43 ± 3.37 mg/L and 210.92 ± 1.00 mg/L for the strains DMKU 7233-1 and DMKUFC10-4, respectively, when the strains were cultivated in a medium amended with 0.1% L-trp. These results were similar to those of other investigations where adding tryptophan to the culture medium enhanced IAA production (Nutaratat et al., 2015; Chen et al., 2022; Bispo et al., 2023). This outcome could be attributed to the role of tryptophan as a biochemical precursor in IAA synthesis (Pedraza et al., 2004; Tsavkelova et al., 2012).

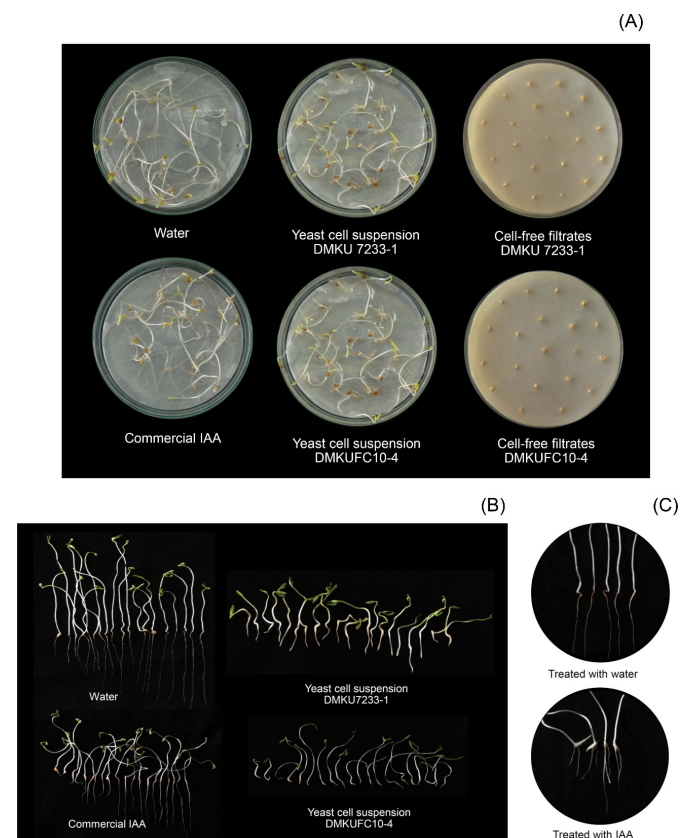


Fig. 4 (A) Effects of indole-3-acetic acid (IAA) produced by marine yeasts *Rhodotorula mucilaginosa* DMKU 7233-1 and *Papiliotrema laurentii* DMKUFC10-4 on tomato seed germination after 7 d, compared with the negative control (water) and positive control (commercial IAA); (B) root and shoot lengths of tomato seedlings following each treatment; (C) visual comparison of tomato roots after treatment with water and IAA.

Table 4 Germination rate, root length, shoot length and stem diameter of tomato seeds after treatment with cell suspension of *Rhodotorula mucilaginosa* or *Papiliotrema laurentii*, compared with negative control (water) and positive control (commercial IAA).

Treatment	Tomato seed germination (%)						Length (mm)		Stem diameter (mm)
	2 DAI	3 DAI	4 DAI	5 DAI	6 DAI	7 DAI	Root	Shoot	
Water	40.0±8.9	95.0±0.0	100±0.0	100±0.0	100±0.0	100±0.0	67.8±2.6 ^a	67.1±1.7 ^a	0.98±0.01 ^b
Commercial IAA	35.0±4.5	91.7±5.2	98.3±2.6	98.3±2.6	100±0.0	100±0.0	30.1±2.1 ^b	54.3±1.0 ^b	0.93±0.03 ^c
Cell suspension of <i>R. mucilaginosa</i> DMKU 7233-1	15.0±4.5	91.7±2.6	98.3±2.6	98.3±2.6	98.3±2.6	98.3±2.6	8.9±0.2 ^c	24.8±0.7 ^c	1.12±0.01 ^a
Cell suspension of <i>P. laurentii</i> DMKUFC10-4	33.3±6.8	91.7±6.8	98.3±2.6	100±0.0	100±0.0	100±0.0	6.6±0.6 ^c	42.4±0.7 ^b	0.90±0.02 ^c

DAI = days after inoculation; IAA = indole-3-acetic acid.

Mean ± SD values followed by different lowercase superscripts letters indicate significant differences ($p < 0.05$) in root length, shoot length, and stem diameter for each treatment. The absence of superscripts letters indicated that statistical analysis was not performed.

Limtong et al. (2014) isolated IAA-producing yeasts from the sugarcane phylloplane and reported that *P. laurentii* had the ability to produce IAA at a concentration of 29.85 ± 0.7 mg/L in a medium without tryptophan. However, its IAA production was reported to be significantly higher in a medium amended with L-trp, reaching 70.97 ± 3.0 mg/L in the presence of 0.1% L-trp (Fu et al., 2016). In addition, *R. mucilaginosa* has been reported as an IAA-producing yeast, with the maximum production when the medium was supplemented with the 0.04% L-trp (Ignatova et al., 2015). Furthermore, Nakayan et al. (2013) reported that *R. mucilaginosa* had low IAA production in a medium in the absence of tryptophan. Based on these and the current results, the marine yeasts *P. laurentii* and *R. mucilaginosa* are promising plant growth promoters, which should be beneficial to agricultural production.

Yeast is known to secrete molecules, such as lytic enzymes, organic acids, phytohormones, siderophores and volatile compounds, which can influence plant growth either directly or indirectly (Nassar et al., 2005; Sun et al., 2014; Freimoser et al., 2019). Siderophores are small compounds produced by various microorganisms with a strong affinity for ferric iron and they promote plant growth by chelating iron and suppress phytopathogenic fungi by depleting environmental iron (Ahmed and Holmström, 2014). However, yeasts having antifungal properties do not always produce siderophores (Nutaratat et al., 2014).

Most of the phosphorus in the soil exists as insoluble phosphate, making it less accessible to plants (Amadou et al., 2022). Phosphorus deficiency can be overcome by applying substantial amounts of fertilizer, which can result in environmental degradation and higher crop production costs. Hence, the phosphate-solubilizing activity of microorganisms plays a crucial role (Sharma et al., 2013). However, in the current study, phosphate-solubilizing activities were not observed in the yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4. This finding was similar to the observations by Fernandez-San Milan et al. (2020), who reported that no yeast strains belonging to the genera *Debaryomyces*, *Issatchenkia*, *Meyerozyma*, *Rhodotorula* and *Torulaspora* had any phosphate-solubilizing ability. On the other hand, catalase helps to break down hydrogen peroxide into oxygen and water, protecting microbes from damage (Kaushal et al., 2018). Yeasts that show catalase activity are likely to survive in the rhizosphere, thereby indirectly promoting plant growth (Martins and English, 2014). Based on the catalase test results in the current study, *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 were positive,

aligning with the findings concerning *R. mucilaginosa* and *P. laurentii* by Chen et al. (2022).

Fungi have a complex cell wall, mostly composed of polysaccharides such as chitin, glucan, glycoprotein and cellulose in some fungal species (Yugueros et al., 2024). A study of cell wall-degrading enzymes reported that *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 could hydrolyze CMC, indicating cellulase activity; however, chitinase activity was not observed. Conversely, protease activity was positive in the yeast *R. mucilaginosa* DMKU 7233-1, but negative in *P. laurentii* DMKUFC10-4. Although, as mentioned above, some cell wall-degrading enzymes were produced by both yeast strains in the current study, these yeasts could not inhibit the mycelial growth of *A. rolfsii*, which causes southern blight of tomatoes (Keinath and DuBose, 2017). Furthermore, Nutaratat et al. (2014) screened yeasts isolated from sugarcane and rice leaves in Thailand for their ability to produce IAA. Their findings implied that while seven IAA-producing isolates also produced cell wall-degrading enzymes, they were not effective in inhibiting the mycelial growth of pathogenic fungi, including *Helminthosporium oryzae*, *Fusarium moniliforme* and *Rhizoctonia solani*.

Low-cost carbon sources are of interest to researchers to improve IAA production yield and subsequently decrease the cost of the production process. Based on the results from the current study, sugarcane molasses was most effective in promoting IAA production by the yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4. Sugarcane molasses is an inexpensive agro-industrial byproduct of the sugar production process and is rich in nutrients and growth factors, with a sugar concentration in the range 40–60%, thus serving as an effective culture medium for fostering microbial growth and producing valuable products (Sineli et al., 2022). Bispo et al. (2023) reported that five out of seven yeast strains belonging to the species *Aureobasidium pullulans*, *Candida pseudointermedia*, *Cryptococcus* sp., *Torulaspora globosa* and *Trichosporon asahii* exhibited effective growth or increased IAA production, or both, when cultivated in a medium containing sugarcane molasses.

Based on the current results, during seedling germination, some lateral roots emerged from the primary root of tomato seeds treated with commercial IAA and yeast cell suspensions of *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4. The effect of IAA on tomato seedlings was also evaluated by Rushabh et al. (2020). They found that the bacterium *Providencia* sp. 7MM11 produced a high amount of IAA (89.22 µg/mL), which resulted in improved germination,

a higher seedling vigor index and greater root and shoot lengths than from the uninoculated control. However, the current results showed that cell-free filtrates, with IAA concentrations of 260.43 ± 3.37 mg/L for strain DMKU 7233-1 and 210.92 ± 1.0 mg/L for strain DMKUFC10-4 did not promote tomato seed germination. The current literature review search revealed that high concentrations of IAA could inhibit plant growth, as noted by Bunsangiam et al. (2021). They reported that 50 mg/L of crude IAA inhibited weed (*Cyperus rotundus* L.) growth. It seems that the utilization of IAA as a plant growth-promoting agent should be optimized; however, at high concentrations, IAA may have herbicidal properties.

Conclusions

The marine yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 isolated from sea sponges showed potential to produce IAA in L-trp-amended and L-trp-free media. Both strains produced catalase and cellulase enzymes; however, neither yeast produced siderophores, ammonia or chitinase, nor did they solubilize phosphate and zinc oxide. In addition, the strain DMKU 7233-1 produced protease enzymes, whereas DMKUFC10-4 did not. There was no antagonistic activity of the marine yeasts *R. mucilaginosa* DMKU 7233-1 and *P. laurentii* DMKUFC10-4 against *A. rolfii*, although some cell wall-degrading enzymes were produced. Growth was promoted in tomato seedlings treated with cell suspensions of the yeast strains DMKU 7233-1 and DMKUFC10-4. However, high concentrations of IAA caused growth inhibition in tomato seedlings. Further studies are required to evaluate the optimum concentration of IAA for promoting seed germination and plant growth.

Conflict of Interest

The authors declare that there are no conflicts of interest.

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