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ENZYMATIC ACTIVITY OF THREE STRAINS FROM TWO *Schizophyllum* SPECIES GROWN ON DIFFERENT SUBSTRATES

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ABSTRACT

Species of the genus *Schizophyllum* have been used in morphogenesis research and in the production of polysaccharides and enzymes. In this study, the growth and enzymatic activity (laccases, amylases, cellulases, pectinases, and xylanases) of two strains of *Schizophyllum commune* and one strain of *Schizophyllum radiatum* were evaluated on different agro-industrial substrates (cedar sawdust, jacaranda sawdust, pine sawdust, peanut shell, coconut fiber, corn stubble, and corn cobs). Growth rate, mycelial characteristics, and enzymatic activity were assessed in Petri dishes. All strains grew on the seven substrates, with higher mycelial density on peanut shells, corn stubble, and corn cobs. The highest enzymatic activity was observed on corn stubble and peanut shell, followed by jacaranda sawdust for amylase, pectinase, and xylanase. *Schizophyllum radiatum* showed greater mycelial extension but lower enzymatic activity than *S. commune* strains. Substrates with lower lignin content (peanut shells, corn stubble, and corn cobs) enhanced growth and enzymatic activity in all strains, indicating that these agro-industrial residues are suitable substrates for obtaining enzyme cocktails from *Schizophyllum* species.

Keywords: corn cobs, corn stubble, laccases, peanut shells, pectinases, xylanases.

INTRODUCTION

Interest in edible and medicinal mushrooms has increased due to their nutritional and nutraceutical value, thereby strengthening research on basidiomycete species for industrial applications. This demand requires improved strategies to optimize the production of fungal metabolites. The culture system influences fungal physiology, growth, and metabolic pathways, modifying the synthesis and secretion of specific metabolites and enzymes. Evidence indicates that solid-state culture can yield higher levels of fungal enzymes at the laboratory scale (Gomes *et al*., 2018).

White-rot fungi can degrade lignin, whereas other fungal groups have limited or no ability to break down lignin but can rapidly decompose other components of plant biomass (Kameshwar and Qin, 2017). Brown-rot fungi primarily break down the polysaccharides of lignocellulose, including cellulose and hemicellulose, while leaving lignin only slightly modified, resulting in a dry brown residue. These fungi have lost the genes encoding class II peroxidases, and depolymerization of plant cell wall polysaccharides occurs mainly through non-enzymatic Fenton reactions generated outside the hyphae (Veloz-Villavicencio *et al*., 2020). Fungal enzymes are essential for the efficient conversion of plant residues. The extracellular enzyme system includes hydrolases (e.g., cellulases, amylases, xylanases) involved in polysaccharide decomposition and phenoloxidases that degrade lignin and open phenyl rings (e.g., laccase, manganese peroxidase, lignin peroxidase, aryl alcohol oxidase). These enzymes have broad biotechnological applications in the food, paper, textile, bioremediation, and cosmetics industries, among others (Ergun and Urek, 2017).

The wood-degrading fungus *Schizophyllum commune* Fr. 1815 is globally distributed and has been recognized as a model organism for research on morphogenesis, gene regulation, and its metabolites (Ohm *et al*., 2010; Pelkmans *et al*., 2016). *Schizophyllum radiatum* Fr. 1851 and *S. commune* were previously considered conspecific based on morphological and genetic similarities (ITS and rDNA). However, multigene analysis has demonstrated that they are separate species that exhibit similar traits and are closely related (Mišković *et al*., 2023). The fruiting bodies of *S. commune* are consumed by various ethnic groups across Asia, Africa, and the Americas (Kamalebo *et al*., 2018). In Mexico, it is traditionally consumed in six southern states (Cappello-García *et al*., 2018). In Tabasco, its consumption and local sale have been documented in the municipalities of Teapa and Macuspana (Ruán-Soto and Cifuentes-Blanco, 2011).

Schizophyllum commune is the most extensively researched species within its genus regarding its biological activity and the characterization of significant molecules. The antitumor activity of polysaccharides from *S. radiatum* has also been examined (López-Legarda *et al*., 2021). *Schizophyllum commune* exhibits a restricted capacity for lignin degradation due to the absence of genes encoding peroxidases, akin to the traits of brown-rot fungi (Ohm *et al*., 2010). This species demonstrates elevated cellulase, xylanase, and pectinase activities, accompanied by diminished laccase activity (Zhu *et al*., 2016). This study assessed the growth and enzymatic activity of three *Schizophyllum* strains cultivated on seven agro-industrial residues to identify fungal strains with significant enzyme production potential.

MATERIALS AND METHODS

Microorganism

Two *S. commune* strains (HEMIM-98 and HEMIM-99) and one *S. radiatum* (HEMIM-107) strain were used. All strains were isolated from wild specimens and were preserved

in the Morelos Mycological Herbarium (HEMIM) collection at the Autonomous University of the State of Morelos. The strains were propagated and maintained on 90 × 15 mm Petri dishes with potato dextrose agar. After the mycelium colonized about 80 % of the surface area of the medium, the cultures were utilized as inoculum.

Culture conditions

Seven agro-industrial wastes were selected based on their lignocellulosic composition: cedar sawdust, jacaranda sawdust, pine sawdust, peanut shells, coconut fiber, corn stubble, and corn cobs. The chopped substrates, approximately 0.5 cm in size, were hydrated for 30 min, resulting in a moisture content of around 76.7, 72, 76.8, 63, 74, 69.2, and 71 % for cedar sawdust, jacaranda sawdust, pine sawdust, peanut shell, coconut fiber, corn stover, and corn cob, respectively. Each substrate was placed into 90 x 15 mm Petri dishes, filling 80 % of the plate volume, and sterilized at 121°C for 20 min. The plates were inoculated with a 5 mm diameter piece of mycelium and incubated in complete darkness at 23–25°C. All assays were performed in triplicate.

Growth speed and mycelial characterization

The mycelial growth velocity (Vc) was determined as the slope of the straight-line equation, obtained from radius measurements taken every 24 h until the mycelium fully colonized the Petri dish. Mycelial characterization was performed on the 17-day-old cultures, assessing texture, density (abundant, regular, or scarce), coloration, and mycelial type (aerial or creeping) for each strain (Sobal *et al*., 2007). All assays were conducted in triplicate.

Enzymatic extracts

Enzymatic extracts (EA) were obtained by adding 25 mL of sterile distilled water per gram of dry substrate colonized by mycelium after 17 d of culture. The mixtures were shaken at 100 rpm for 20 min and refrigerated at 4 °C for 24 h. After this period, they were centrifuged at 20 000 × g for 10 min at 2 °C using a HERMLE Z36HK centrifuge, and then stored at -20 °C until use.

Enzymatic activities

Laccase activity was evaluated in triplicate using 2,6-dimethoxyphenol (DMP) as the substrate. The reaction mixture comprised 950 µL of the substrate (2 mM DMP in 0.1 M acetate buffer, at pH 4.0, 4.5, 5.0, 5.5) and 50 µL of EA, incubated for 5 min at 40 °C. The absorbance was subsequently measured at 468 nm using a UV-Vis spectrophotometer (L6S). The activity unit (U) of laccases was defined as the quantity of enzyme that generates an increase of one absorbance unit per minute in the reaction mixture. Activity was expressed as U gX^{-1} (U per gram of dry agro-industrial waste colonized by mycelium) (Téllez-Téllez *et al*., 2008).

The activities of amylases, cellulases, pectinases, and xylanases were assessed using starch, carboxymethylcellulose, polygalacturonic acid, and birch xylan, with

all substrates dissolved at 1 % in 0.1 M acetate buffer at pH 5.0. Reaction mixtures consisting of 950 µL of substrate and 50 µL of EA were incubated at 50 °C for 45 min. The release of reducing sugars was quantified using the dinitrosalicylic acid (DNS) method, with absorbance measured at 575 nm (Miller, 1959). In all cases, one U was defined as the amount of enzyme that released one µmol of reaction product per minute under assay conditions (in U gX^{-1}). All tests were conducted in triplicate.

Statistical analysis

All analyses were performed in triplicate, and mean values were used for statistical analysis. Data were analyzed using SigmaStat software (Systat Software Inc., Palo Alto, CA, USA). Differences among treatments were assessed by one-way analysis of variance (ANOVA) and Tukey's test ($p < 0.05$).

RESULTS AND DISCUSSION

Mycelial growth rate and characterization

In general, the *S. radiatum* strain exhibited higher Vc values than both *S. commune* strains (Table 1). Corn stubble exhibited the highest Vc values for all three strains, whereas pine sawdust resulted in the lowest Vc values. The three lignin-rich substrates exhibited the lowest Vc values.

Regarding the morphological characteristics observed (Table 2), the mycelium on peanut shells, corn stover, and corn cobs exhibited a white hue, a cottony texture, and a density ranging from regular to abundant. In contrast, all three sawdust substrates, as well as the coconut fiber, exhibited hyaline mycelium with an inconspicuous texture and very low (near-zero) density.

Table 1. Mycelial growth velocity of the evaluated *Schizophyllum* strains on various agro-industrial waste substrates.

Substrate	Mycelial growth rate (mm h^{-1})*		
	S. commune HEMIM-98	*S. commune* HEMIM-99	*S. radiatum* HEMIM-107
Cedar sawdust	0.152 (0.004)c	0.178 (0.002)b	0.205 (0.001)c
Jacaranda sawdust	0.178 (0.008)b	0.171 (0.003)b	0.261 (0.015)b
Pine sawdust	0.149 (0.006)c	0.165 (0.016)b	0.194 (0.008)c
Peanut shells	0.181 (0.006)b	0.172 (0.005)b	0.264 (0.022)b
Coconut fiber	0.178 (0.006)b	0.177 (0.012)b	0.226 (0.012)c
Corn stubble	0.206 (0.002)a	0.203 (0.006)a	0.302 (0.005)a
Corn cob	0.173 (0.003)b	0.185 (0.006)b	0.225 (0.007)c

*Mean values per column with different letters are statistically different ($p \leq 0.05$). Standard error is shown in parentheses.

Table 2. Mycelium characteristics of the evaluated *Schizophyllum* strains grown on various agro-industrial substrates.

Substrate	Characteristics				
	Color	Texture	Type of mycelium	Density	Hyphal aggregation
		S. commune HEMIM-98			
Cedar sawdust	Hyaline	Absent	Aerial	Low	Absent
Jacaranda sawdust	Hyaline	Absent	Aerial	Low	Present
Pine sawdust	Hyaline	Absent	Aerial	Low	Present
Peanut shell	White	Cottony	Aerial	Middle	Present
Coconut fiber	Hyaline	Absent	Creeping	Low	Absent
Corn stubble	White	Cottony	Aerial	High	Present
Corn cob	White	Cottony	Aerial	Middle	Absent
		S. commune HEMIM-99			
Cedar sawdust	Hyaline	Absent	Aerial	Low	Absent
Jacaranda sawdust	Hyaline	Absent	Aerial	Low	Absent
Pine sawdust	Hyaline	Absent	Aerial	Low	Absent
Peanut shell	White	Cottony	Aerial	Middle	Present
Coconut fiber	Hyaline	Absent	Creeping	Low	Absent
Corn stubble	White	Cottony	Aerial	High	Present
Corn cob	White	Cottony	Aerial	Middle	Absent
		S. radiatum HEMIM-107			
Cedar sawdust	Hyaline	Absent	Aerial	Low	Absent
Jacaranda sawdust	Hyaline	Absent	Creeping	Middle	Absent
Pine sawdust	Hyaline	Cottony	Creeping	Middle	Absent
Peanut shell	Hyaline	Cottony	Aerial	High	Present
Coconut fiber	Hyaline	Absent	Creeping	Low	Absent
Corn stubble	White	Cottony	Aerial	High	Absent
Corn cob	White	Cottony	Aerial	High	Absent

The best substrates for the three strains, based on mycelial density, were peanut shells, corn stubble and corn cob (Figures 1, 2 and 3), with total invasion occurring after 6–10 d. In the other substrates, total invasion occurred after 7–12 d. *Schizophyllum commune* HEMIM-98 presented fruiting bodies and spores after 20 d of growth (Figure 4).

Previous studies have reported the growth of *S. commune* on agro-industrial substrates incubated at 28 °C under dark conditions. The fastest growth occurred in cocoa shells (0.4 mm h^{-1}), banana leaves (0.41 mm h^{-1}), and mixed substrates of coconut-cocoa (0.42 mm h^{-1}), cocoa-banana (0.41 mm h^{-1}), coconut-cocoa (0.42 mm h^{-1}), and cocoa-banana (0.41 mm h^{-1}), with no statistically significant differences observed (Carreño-Ruiz *et al*., 2014).

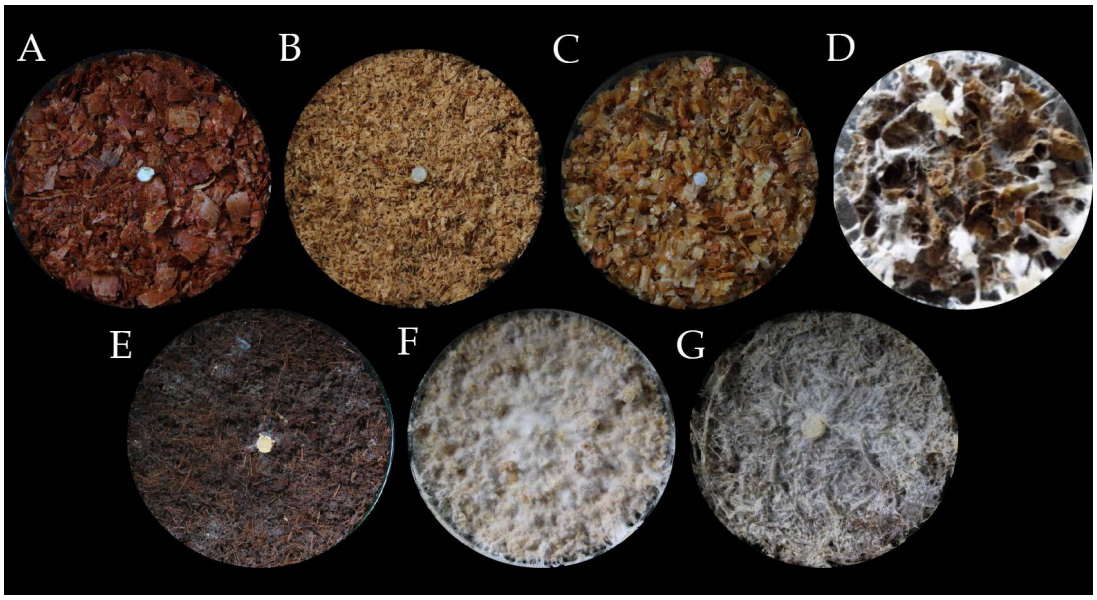

Figure 1. Mycelial growth of *Schizophyllum commune* HEMIM-98 on different substrates. A: cedar sawdust; B: jacaranda sawdust; C: pine sawdust; D: peanut shell; E: coconut fiber; F: corn stubble; G: corn cob.

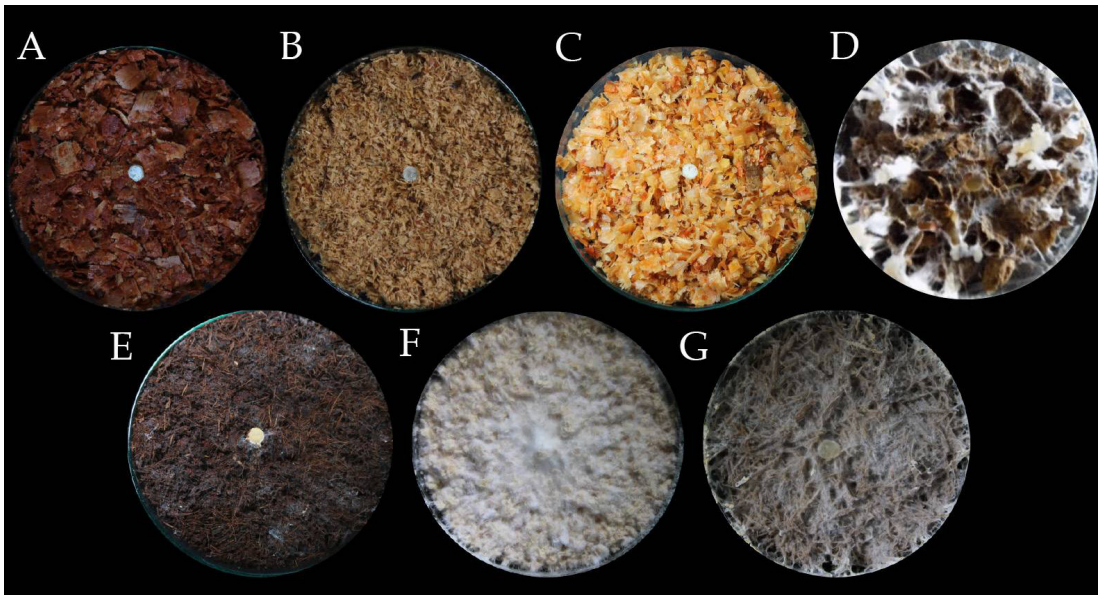

Figure 2. Mycelial growth of *Schizophyllum commune* HEMIM-99 on different substrates. A: cedar sawdust; B: jacaranda sawdust; C: pine sawdust; D: peanut shell; E: coconut fiber; F: corn stubble; G: corn cob.

Figure 3. Mycelial growth of *Schizophyllum radiatum* HEMIM-107 on different substrates. A: cedar sawdust; B: jacaranda sawdust; C: pine sawdust; D: peanut shell; E: coconut fiber; F: corn stubble; G: corn cob.

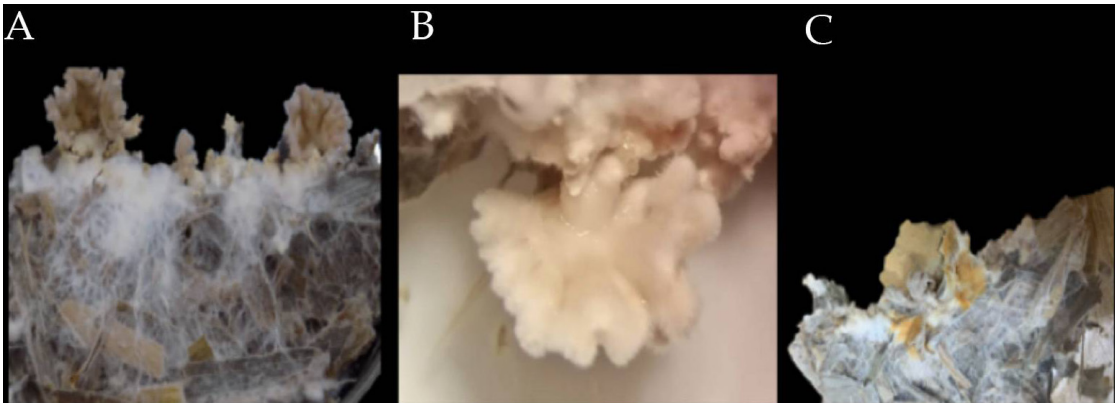

Figure 4. Fruiting bodies and sporulation of *Schizophyllum commune* HEMIM-98 grown on corn stover in Petri dishes. A, B: Fruiting body; C: spores.

In another study, Carreño-Ruiz *et al*. (2020) cultivated four *S. commune* strains on cocoa shells, banana leaves, corn leaves, and mulatto sticks. All strains showed accelerated growth on mulatto stick (Vc = 0.41 mm h^{-1}). One strain attained a Vc value of 0.195 mm h^{-1} on banana leaves, whereas the other three strains cultivated on corn leaves exhibited Vc values of 0.056, 0.098, and 0.17 mm h^{-1}. The authors proposed that *S. commune* exhibited greater growth on mulatto sticks due to their status as a natural host. However, its use as a substrate is not feasible due to the ecological and economic implications of removing the tree from the natural environment (Ruan-Soto *et al*., 2004).

Enzymatic activity

All strains presented enzymatic activities for the five tests assessed, with xylanase activity typically yielding the highest values. The *S. radiatum* strain showed the lowest laccase and pectinase activities but ranked second in xylanase activity. The three strains demonstrated amylase activity (Figure 5A), with *S. commune* HEMIM-99 exhibiting the highest value and *S. radiatum* the lowest, both cultivated on jacaranda sawdust (10.26 and 0.27 U gX^{-1}, respectively). However, *S. radiatum* reached its maximum amylase activity when grown on corn stover (6.77 U gX^{-1}). For cellulase activity, the best substrates for all strains were peanut shells and corn stubble (Figure 5B). The HEMIM-99 strain grown on the three types of sawdust did not exhibit cellulase activity and had minimal activity when grown on coconut fiber and corn cobs. Meanwhile, *S. commune* HEMIM-98 and *S. radiatum* had the highest cellulase activity on corn stover (14.97 and 6.69 U gX^{-1}, respectively), whereas HEMIM-99 reached its maximum cellulase activity on peanut shells (9.02 U gX^{-1}).

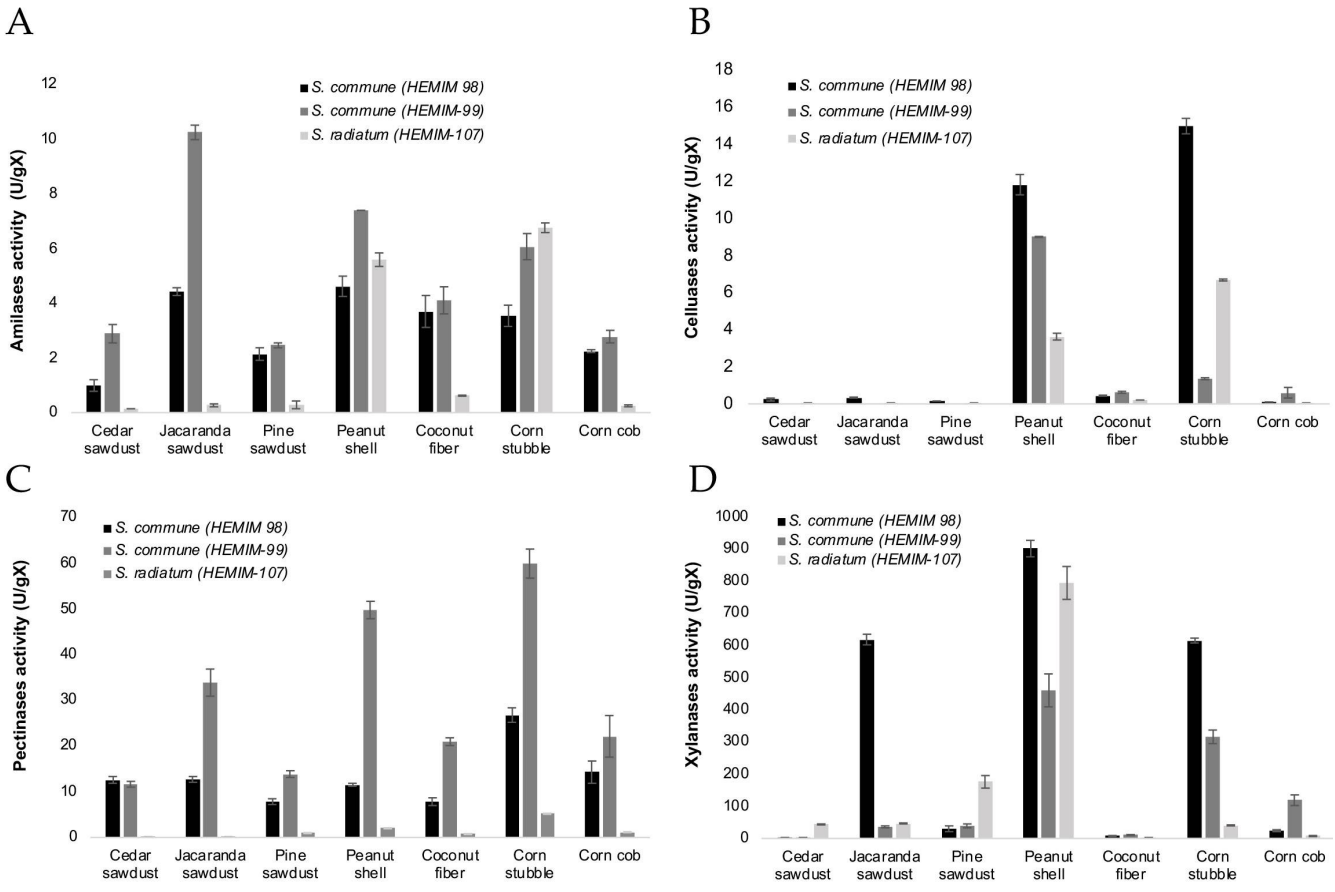

Figure 5. Enzymatic activity of the evaluated *Schizophyllum* strains grown on different agro-industrial residues. A: Amylases; B: cellulases; C: pectinases; D: xylanases.

The pectinase activity of the *S. radiatum* strain was minimal to undetectable on all evaluated substrates, while both *S. commune* strains exhibited measurable activity when grown on all substrates; HEMIM-98 had values between 10 and 26 U gX^{-1}, and HEMIM-99 had its highest value at 59.83 U gX^{-1} on corn stubble (Figure 5C). Peanut shells served as the best substrate for xylanase activity across all three strains, yielding values of 900, 459, and 795 U gX^{-1} for HEMIM-98, HEMIM-99, and HEMIM-107, respectively (Figure 5D). Corn stubble also provided significant xylanase activity, with values of 615, 317, 176 U gX^{-1} for HEMIM-98, HEMIM-99, and HEMIM-107, respectively. The lowest xylanase activity was found for HEMIM-107 (4.3 U gX^{-1}) grown on coconut fiber, while *S. commune* grown on cedar sawdust achieved values of 2.86 and 2.09 U gX^{-1} for HEMIM-98 and HEMIM-99, respectively.

Regarding laccase activity, the three strains demonstrated elevated activity at pH 5.0 and 5.5; *S. commune* HEMIM 98 exhibited the highest activity, while *S. radiatum* had the lowest (Figure 6). The highest laccase activity recorded for the three strains occurred on corn stubble, reaching 23.6 U gX^{-1} (HEMIM-98), 17.7 U gX^{-1} (HEMIM-99), and 10.29 U gX^{-1} (HEMIM-107), followed by coconut fiber with 1.46, 2.33, and 0.8 U gX^{-1}, respectively. On all other substrates, laccase activity was less than 2 U gX^{-1} (Figure 6).

In general, the substrates that favored fungal growth, mycelium density, and hydrolytic enzymatic activity (amylases, pectinases, cellulases and xylanases) were those with the lowest lignin content. Corn stubble contains 6.8 % lignin, 27.6 % hemicellulose, and 45.5 % cellulose (Costa *et al*., 2015); corn cobs contain 15 % lignin, 35 % hemicellulose, and 45 % cellulose (Garrote *et al*., 2007); and peanut shells contain 27 % lignin, 30 % hemicellulose, and 45 % cellulose (Gatani *et al*., 2010). In the case of laccase activity, corn stubble and coconut fiber were also the most favorable substrates. Coconut fiber contains 41 % lignin, 16.3 % hemicellulose, and 31.2 % cellulose (Abdullah *et al*., 2021).

In recent decades, several studies have explored the use of agro-industrial waste as raw materials for the production of value-added products. Fungal enzymes participate in the degradation of these solid substrates to supply a source of carbon and mineral nutrients for fungal growth. Cellulases, xylanases, pectinases, and ligninases participate in the degradation of lignocellulosic substrates (Gomes *et al*., 2018). In *S. commune*, the production of several industrially important enzymes has been reported, including cellulases, xylanases, pectinases, lipases, laccases, manganese peroxidase, and lignin peroxidase (Kam *et al*., 2016; Sornlake *et al*., 2017; Gautam *et al*., 2018; Kumar *et al*., 2018; Mehmood *et al*., 2018).

The genome of *S. commune* contains 16 genes encoding lignin oxidative enzymes (FOLymes), including one cellobiose dehydrogenase, one aryl alcohol oxidase, one alcohol oxidase, two laccases, one glyoxal oxidase, and four benzoquinone reductases (Ohm *et al*., 2010). It also has vast enzymatic machinery to degrade cellulose, pectin, and hemicellulose. In total, 240 glycoside hydrolases, 75 glycosyltransferases, 16 polysaccharide lyases, and 30 carbohydrate esterases have been identified, totaling 366 carbohydrate-active enzymes (CAZymes), of which 106 are presumed to be involved in plant polysaccharide degradation. Although *S. commune* is sometimes classified as

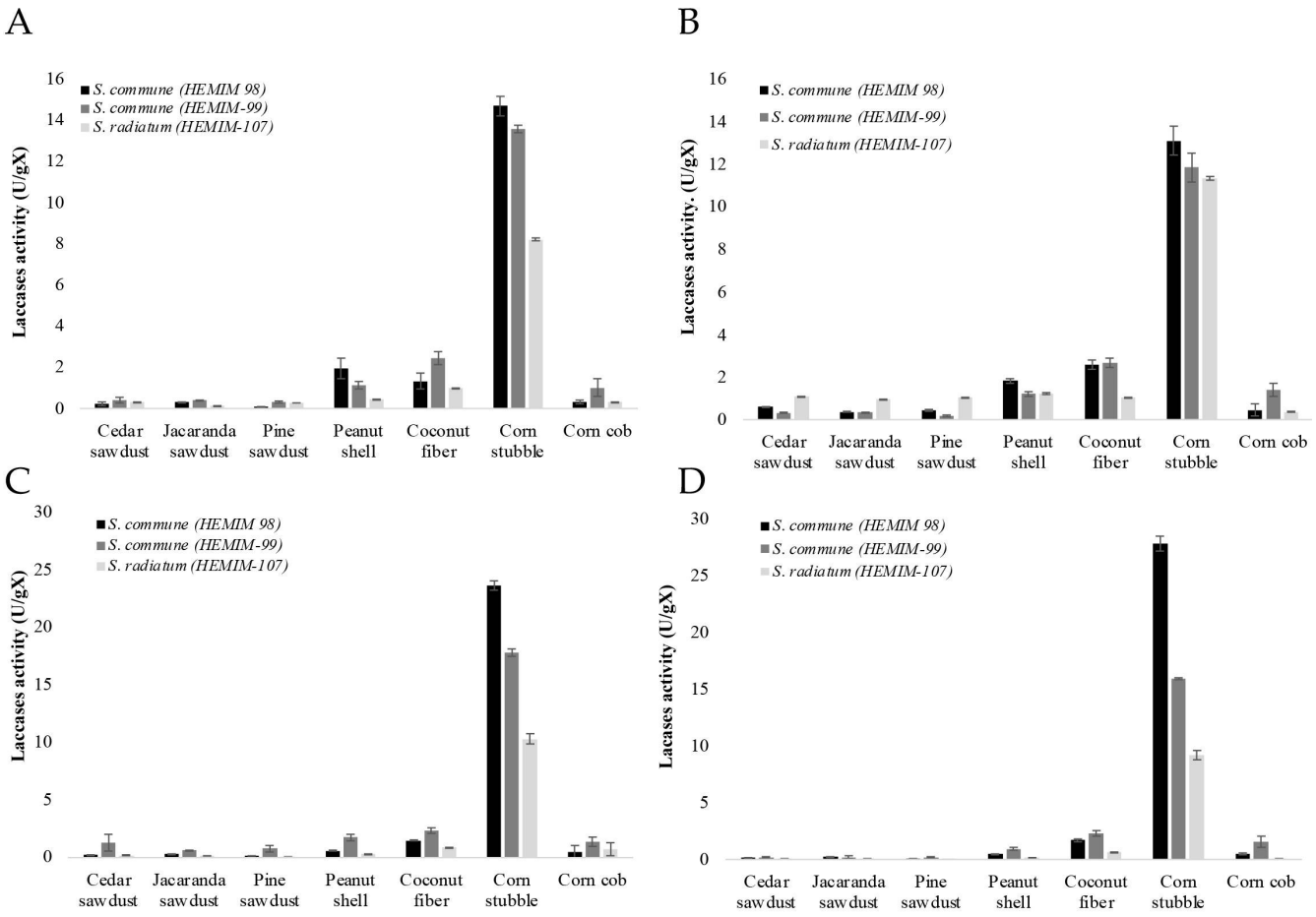

Figure 6. Laccase activity of the evaluated *Schizophyllum* strains grown on different agro-industrial residues. A: pH 4.0; B: pH 4.5; C: pH 5.0; D: pH 5.5.

a white-rot fungus, it does not significantly degrade lignin *in vitro*. The genome lacks class II peroxidases and contains a reduced set of enzymes with cellulose-binding modules. However, it encodes 22 lytic polysaccharide monooxygenases. Due to these characteristics, *S. commune* exhibits a decay mode between dark-rot fungi and has been considered an intermediate between white- and dark-rot fungi (Riley *et al*., 2014). Zhu *et al*. (2016) reported that *S. commune* excretes a broad set of extracellular enzymes involved in the degradation of plant cell wall components. Their study identified increased activities of several enzymes during cultivation, including endoglucanase, cellobiohydrolase, β-glucosidase, polygalacturonase, β-xylosidase, and xylanase. These findings suggest that lignocellulose degradation by *S. commune* involves a hydroxyl radical-mediated mechanism for lignocellulose modification, in parallel with a synergistic system of several enzymes that degrade polysaccharides. Sornlake *et al*.

(2017) evaluated the hydrolytic efficiency of enzymes produced by *S. commune* G-135, which contain glycosyl hydrolases. One mutant (Avicel-PH101) efficiently hydrolyzed several lignocellulosic residues, with the highest values reported in corn cobs (98 %), and a significant improvement in xylan conversion. In this study, overall corn stubble yielded the highest enzymatic activities, although corn cob was suitable for producing amylases and pectinases.

Arunrattanamook *et al*. (2022) reported that the maximum enzymatic activity of *S. commune* was reached on the second day of cultivation and remained stable until day seven. This period coincided with the onset of extracellular polysaccharide production. At the highest levels of these polysaccharides, xylanase activity reached its minimum, indicating that this activity is not directly associated with fungal growth. Singh *et al*. (2017) reported that nutrient depletion began after 5 d of liquid cultivation of *S. commune*. The lignocellulolytic enzyme system was activated, increasing protein content and enabling enzymatic degradation of cellulose and hemicellulose, thereby increasing the concentration of reducing sugars in the medium and favoring the growth of the fungus.

Kondaveeti *et al*. (2020) reported two cellobiohydrolase enzymes from *S. commune* KMJ820 obtained by liquid culture of approximately 50 and 150 kDa; these enzymes stand out compared to other cellobiohydrolases for their high enzymatic activity and their potential for large-scale production of glucose or ethanol by biological methods. Faheem *et al*. (2023) purified and characterized a ρ-diphenol oxidase from *S. commune* (MF-O5); the enzyme demonstrated tolerance to salt, metal ions, organic solvents, and surfactants, highlighting its potential for use in various industrial applications.

CONCLUSIONS

Schizophyllum strains grow on economically accessible substrates, enabling the production of enzymatic cocktails for diverse biotechnological applications. Peanut shells, corn stubble, and corn cobs are abundant agro-industrial wastes, making them accessible. Their use as substrates for fungal growth and enzyme production offers a sustainable alternative for generating value-added products while preventing them from contributing to organic matter accumulation. This study constitutes the first report on enzyme production by *S. radiatum*, demonstrating its potential as an alternative to *S. commune*. Although *S. radiatum* exhibits comparatively lower enzymatic activity, its rapid growth makes it a viable and efficient option for biotechnological applications.

REFERENCES

Abdullah NA, Sainorudin MH, Rani MSA, Mohammad M, Kadir NH, Asim N. 2021. Structure and thermal properties of microcrystalline cellulose extracted from coconut husk fiber. Polimery 66 (3): 187–192. https://doi.org/10.14314/polimery.2021.3.4

Arunrattanamook N, Sornlake W, Champreda V. 2022. Co-production of schizophyllan and cellulolytic enzymes from bagasse by *Schizophyllum commune*. Bioscience, Biotechnology, and Biochemistry 86 (8): 1144–1150. https://doi.org/10.1093/bbb/zbac091

Cappello-García S, Carreño-Ruíz SD, Gaitán-Hernández R. 2018. Fruit body production of *Schizophyllum commune*. *In* Sánchez JE, Mata G, Royse DJ. (eds.), Updates on Tropical Mushrooms. Basic and Applied Research. El Colegio de la Frontera Sur: San Cristóbal de las Casas, Mexico, pp: 95–104.

Carreño-Ruiz SD, Cappello-García S, Gaitán-Hernández R, Cifuentes-Blanco J, Rosique-Gil E. 2014. Growth of three tropical edible fungi in culture mediums and agricultural waste. Revista Mexicana de Ciencias Agrícolas 5 (8): 1447–1458. https://doi.org/10.29312/remexca.v5i8.822

Carreño-Ruiz SD, Cappello-García S, Gaitán-Hernández R, Torres-de la Cruz M, Gaspar-Génico JA, Rosique-Gil JE. 2020. Producción de basidiomas de Schizophyllum commune (Fungi: Basidiomycota) en subproductos agrícolas de Tabasco, México. AgroProductividad 13 (5): 65–71.

Costa LAS, Assis DJ, Gomes GVP, da Silva JBA, Fonsêca AF, Druzian JI. 2015. Extraction and characterization of cellulose nanocrystals from corn stover. Cellulose Chemistry and Technology 49 (2): 127–133. https://doi.org/10.1016/j.matpr.2015.04.045

Ergun SO, Urek RO. 2017. Production of ligninolytic enzymes by solid state fermentation using *Pleurotus ostreatus*. Annals of Agrarian Science 15 (2): 273–277. https://doi.org/10.1016/j.aasci.2017.04.003

Faheem M, Bokhari SAI, Malik MA, Ahmad B, Riaz M, Zahid N, Hussain A, Ghani A, Ullah H, Shah W, *et al*. 2023. Production, purification, and characterization of p-diphenol oxidase (PDO) enzyme from lignolytic fungal isolate *Schizophyllum commune* MF-O5. Folia Microbiologica 68 (6): 867–888. https://doi.org/10.1007/s12223-023-01056-w

Garrote G, Falqué E, Domínguez H, Parajó JC. 2007. Autohydrolysis of agricultural residues: Study of reaction byproducts. Bioresource Technology 98 (10): 1951–1957. https://doi.org/10.1016/j.biortech.2006.07.049

Gatani M, Argüello R, Sesín S. 2010. Effect of chemical treatments on the mechanical properties of peanut shell and cement blends. Materiales de Construcción 60 (298): 137–147. https://doi.org/10.3989/mc.2010.46908

Gautam A, Kumar A, Bharti AK, Dutt D. 2018. Rice straw fermentation by *Schizophyllum commune* ARC-11 to produce high level of xylanase for its application in pre-bleaching. Journal of Genetic Engineering and Biotechnology 16 (2): 693–701. https://doi.org/10.1016/j.jgeb.2018.02.006

Gomes E, da Silva R, de Cassia Pereira J, Ladino-Orjuela G. 2018. Fungal growth on solid substrates: A physiological overview. *In* Pandey A, Larroche C, Soccol CR. (eds.), Current Developments in Biotechnology and Bioengineering. Elsevier: Amsterdam, Netherlands, pp: 31–56. https://doi.org/10.1016/B978-0-444-63990-5.00003-7

Kam YC, Hii SL, Sim CY, Gaik L, Ong A. 2016. *Schizophyllum commune* lipase production on pretreated sugarcane bagasse and its effectiveness. International Journal of Polymer Science 2016 (1): 2918202. https://doi.org/10.1155/2016/2918202

Kamalebo HM, Wa Malale HNS, Ndabaga CM, Degreef J, Kesel AD. 2018. Uses and importance of wild fungi: Traditional knowledge from the Tshopo province in the Democratic Republic of the Congo. Journal of Ethnobiology Ethnomedicine 14 (1). https://doi.org/10.1186/s13002-017-0203-6

Kameshwar AKS, Qin W. 2017. Qualitative and quantitative methods for isolation and characterization of lignin-modifying enzymes secreted by microorganisms. Bioenergy Research 10 (1): 248–266. https://doi.org/10.1007/s12155-016-9784-5

Kondaveeti S, Patel SKS, Woo J, Wee JH, Kim SY, Al-Raoush RI, Kim IW, Kalia VC, Lee JK. 2020. Characterization of cellobiohydrolases from *Schizophyllum commune* KMJ820. Indian Journal of Microbiology 60 (2): 160–166. https://doi.org/10.1007/s12088-019-00843-9

Kumar B, Bhardwaj N, Alam A, Agrawal K, Prasad H, Verma P. 2018. Production, purification and characterization of an acid/alkali and thermo tolerant cellulase from *Schizophyllum commune* NAIMCC-F-03379 and its application in hydrolysis of lignocellulosic wastes. AMB Express 8 (1): 173. https://doi.org/10.1186/s13568-018-0696-y

López-Legarda X, Rostro-Alanis M, Parra-Saldivar R, Villa-Pulgarín JA, Segura-Sánchez F. 2021. Submerged cultivation, characterization and *in vitro* antitumor activity of polysaccharides from *Schizophyllum radiatum*. International Journal of Biological Macromolecules 186: 919–932. https://doi.org/10.1016/j.ijbiomac.2021.07.084

Mehmood T, Saman T, Irfan M, Anwar F, Salman M, Tabassam Q. 2018. Pectinase production from *Schizophyllum commune* through central composite design using citrus waste and its immobilization for industrial exploitation. Waste Biomass Valorization 10 (9): 2527–2536. https://doi.org/10.1007/s12649-018-0279-9

Miller GL. 1959. Use of dinitrosalicylic acid reagent for determination of reducing sugar. Analytical Chemistry 31 (3): 426–428. https://doi.org/10.1021/ac60147a030

Mišković J, Rašeta M, Krsmanović N, Karaman M. 2023. Update on mycochemical profile and selected biological activities of genus *Schizophyllum* Fr. 1815. Microbiology Research 14 (1): 409–429. https://doi.org/10.3390/microbiolres14010031

Ohm RA, de Jong JF, Lugones LG, Aerts A, Kothe E, Stajich JE, de Vries RP, Record E, Levasseur A, Baker SE, *et al*. 2010. Genome sequence of the model mushroom *Schizophyllum commune*. Nature Biotechnology 28 (9): 957–963. https://doi.org/10.1038/nbt.1643

Pelkmans J, Lugones L, Wösten HA. 2016. Fruiting body formation in basidiomycetes. *In* Wendland J. (ed.), Growth, Differentiation and Sexuality. The Mycota, vol 1. Springer: Cham, Switzerland, pp: 387–405. https://doi.org/10.1007/978-3-319-25844-7_15

Riley R, Salamov AA, Brown D, Nagy LG, Floudas D, Held BW, Levasseur A, Lombard V, Morin E, Otillar R, *et al*. 2014. Extensive sampling of basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. Proceedings of the National Academy of Sciences 111 (27): 9923–9928. https://doi.org/10.1073/pnas.1400592111

Ruán-Soto F, Cifuentes-Blanco J. 2011. Notas etnomicológicas del poblado de Teapa, Tabasco. *In* López-Hernández ES, Ruiz-Macdonel MA. (eds.), Educación Ambiental para la Conservación de la Biodiversidad. El Colegio de Investigadores de Tabasco A.C. Villahermosa, México, pp: 249–256

Ruan-Soto F, Garibay-Orijel R, Cifuentes-Blanco J. 2004. Conocimiento micológico tradicional en la planicie costera del Golfo de México. Revista Mexicana de Micología 19: 57–70.

Singh MK, Kumar M, Thakur IS. 2017. Proteomic characterization and schizophyllan production by *Schizophyllum commune* ISTL04 cultured on *Leucaena leucocephala* wood under submerged fermentation. Bioresource Technology 236: 29–36. https://doi.org/10.1016/j.biortech.2017.03.170

Sobal M, Martínez-Carrera D, Morales P, Roussos S. 2007. Classical characterization of mushroom genetic resources from temperate and tropical regions of Mexico. Micología Aplicada Internacional 19 (1): 15–23.

Sornlake W, Rattanaphanjak P, Champreda V, Eurwilaichitr L, Kittisenachai S, Roytrakul S, Fujii T, Inoue H. 2017. Characterization of cellulolytic enzyme system of *Schizophyllum commune* mutant and evaluation of its efficiency on biomass hydrolysis. Bioscience, Biotechnology and Biochemistry 81 (7): 1289–1299. https://doi.org/10.1080/09168451.2017.1320937

Téllez-Téllez M, Fernández FJ, Montiel-González AM, Sánchez C, Díaz-Godínez G. 2008. Growth and laccase production by *Pleurotus ostreatus* in submerged and solid-state fermentation. Applied Microbiology Biotechnology 81 (4): 675–679. https://doi.org/10.1007/s00253-008-1628-6

Veloz-Villavicencio E, Mali T, Mattila HK, Lundell T. 2020. Enzyme activity profiles produced on wood and straw by four fungi of different decay strategies. Microorganisms 8 (1): 73. https://doi.org/10.3390/microorganisms8010073

Zhu N, Liu J, Yang J, Lin Y, Yang Y, Ji L, Li M, Yuan H. 2016. Comparative analysis of the secretomes of *Schizophyllum commune* and other wood-decay basidiomycetes during solid-state fermentation reveals its unique lignocellulose-degrading enzyme system. Biotechnology for Biofuels 9 (42): 1–22. https://doi.org/10.1186/s13068-016-0461-x