# Influence of Different Lignocellulosic Materials on Laccase Activity in Liquid Fermentation of Chinese Low-temperature Straw Mushroom (*Volvariella brumalis*)

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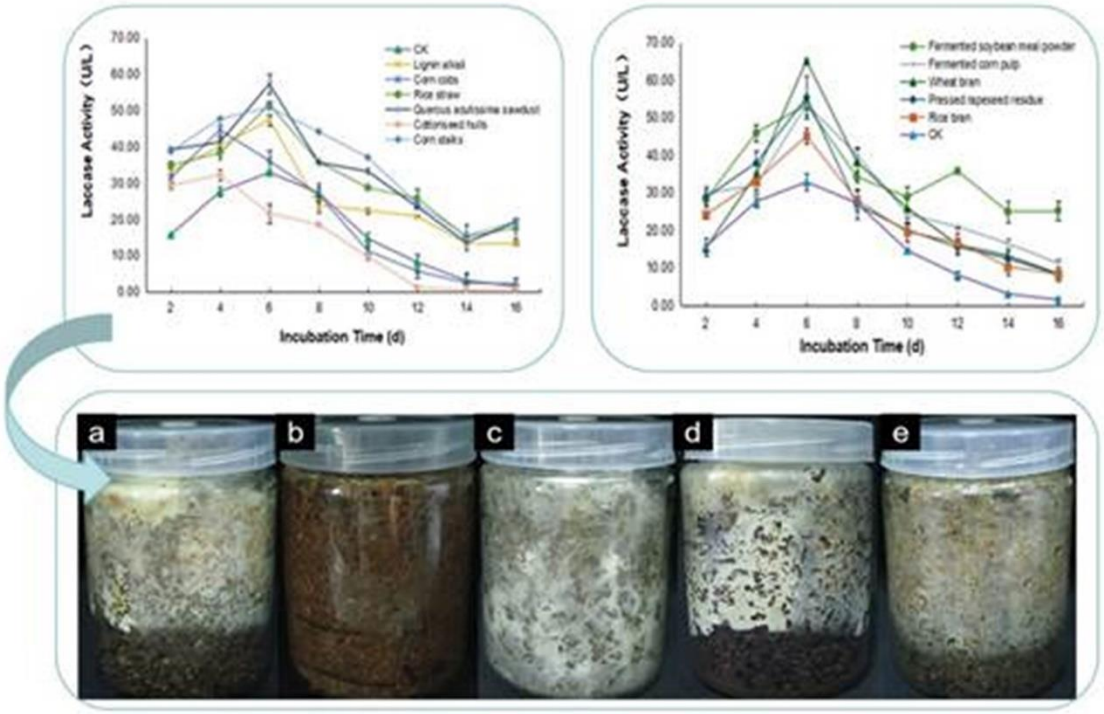
## GRAPHICAL ABSTRACT



# Influence of Different Lignocellulosic Materials on Laccase Activity in Liquid Fermentation of Chinese Low-temperature Straw Mushroom (*Volvariella brumalis*)

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The laccase activity of a low-temperature strain of *Volvariella brumalis* was studied using different lignocellulosic biomasses for liquid fermentation. The results showed that the laccase activity induced by wheat bran or pressed rapeseed residue was higher than the other auxiliary cultivation substrates. Compared to other primary cultivation substrates, *Quercus acutissima* sawdust and rice straw not only stimulated *V. brumalis* to produce more laccase in liquid fermentation, but also promoted better mycelial growth in solid-state fermentation. Therefore, these agricultural and forestry wastes should be prioritized as culturing materials of *V. brumalis* for laccase high-secretion and hyphal growth to increase production of *V. brumalis*.

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*Keywords: Volvariella brumalis; Lignocellulose; Liquid fermentation; Laccase activity; Culturing formulas*

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## INTRODUCTION

The by-products from woodworking, forestry, agriculture, and fermentation industries were once considered as wastes. Recent research has shown that lignocellulose derived from these agricultural and forestry wastes can be regarded as a promising resource for sustainable energy production (Lynd *et al.* 2008; Gao *et al.* 2022; Kondaveeti *et al.* 2022; Chen *et al.* 2023; Kaur *et al.* 2023; Madadi *et al*. 2023; Shrivastava and Sharma 2023). However, the first step to effectively utilize lignocellulose is to remove lignin, which hinders cellulose saccharification (Gaikwad and Meshram 2020; Govil *et al*. 2022; Jindal *et al.* 2023). White-rot fungi are recognized as effective lignocellulose degraders in nature and are known as the producers of lignin-degrading enzymes (Manavalan *et al.* 2015; Martani *et al.* 2017; Chen *et al.* 2022; Echezonachi 2022; Wu *et al.* 2024). Laccase with high lignin-degrading capability is the most important enzyme among ligninolytic enzymes in extensive studies (Agrawal *et al*. 2018; Nunes and Kunamneni 2018; Lira-Pérez *et al*. 2020; Chen *et al.* 2022; Li *et al.* 2023). Many white-rot fungi with the capacity to secrete laccase are high in their edible and medicinal values (Sun *et al.* 2011; Cesur *et al.* 2022; Lou *et al.* 2023; Hazelgrove and Moody 2024). Moreover, all the edible fungi that can be farmed with various agricultural and forestry wastes not only facilitate development of the edible fungal industry, but they also enhance the secondary resources utilization. For example, wood chips, rice straw, wheat straw, corn cob, corn stalks, coffee shell, sugarcane bagasse, cottonseed shell, wheat bran, and rice bran could be used to cultivate edible fungi

(Luo and Chen 2010). At the same time, these lignocellulosic biomasses could stimulate fungi to produce laccase (Elisashvili *et al*. 2008; Huang *et al*. 2019; Wang *et al*. 2019; An *et al*. 2020a; Atilano-Camino *et al*. 2020; Pinheiro *et al*. 2020; Agrawal and Verma 2022; Ahmed *et al*. 2022). The mycelial growth and fruiting bodies development are closely related to the laccase activity in edible mushrooms (Chen 2003; Chen *et al.* 2004a,b; Sun *et al.* 2011; Cesur *et al.* 2022). The edible mushroom strains secreting high levels of laccase also have shorter growth cycles (Sun *et al.* 2011). The mycelial growth and fruiting body development stages of *Volvariella volvacea* are accompanied by significant expression of laccase genes (Chen *et al.* 2004a,b). Additionally, laccase activity is relatively low during the mycelial stage of *V. volvacea*, but high during primordium formation and fruiting body development stages (Chen 2003). Straw mushrooms are typically edible fungi with significant market demands (Luo and Chen 2010). The straw mushroom strains can be selected based on the activity of extracellular lignocellulolytic enzymes, with laccase activity being one of the evaluation criteria (Ahlawat *et al.* 2008). *Volvariella brumalis*, a low temperature straw mushroom, could form fruiting bodies at temperatures ranging from 4 to 17 °C (He and Feng 1987; Lian *et al*. 1998). A strain of *V*. *brumalis* can grow well at temperatures ranging from 10 to 25 °C. At temperatures ranging from 0 to 5 °C the fungus does not germinate but remains viable (Li *et al*. 2022). These biological characteristics mean that *V. brumalis* may have a longer shelf life than *V. volvacea* and *V. bombycina*, with great potential to meet the winter market demand for straw mushrooms (Luo and Chen 2010; Ahlawat *et al*. 2016; Khan *et al*. 2021).

At the edible mushroom farm in Liupanshui City, China, where sawdust was being used as the main substrate for cultivating *Stropharia rugosoannulata*, many fruitbodies of wild *V. brumalis* were found. This suggests that *V. brumalis*, like *V. bombycina*, may have a certain preference for sawdust. This phenomenon is unusual in the species of the genus *Volvariella* (Luo and Chen 2010). Therefore, agricultural and forestry waste commonly used for cultivating straw mushrooms was utilized in this experiment to stimulate laccase production in *V. brumalis* through liquid fermentation (Luo and Chen 2010). The aim of this study is to select and analyze the main and auxiliary materials in cultivation formulas for inducing high laccase secretion, thereby promoting faster and better mycelial growth of *V. brumalis*. This will lay the foundation for improving quality and increasing yield in *V. brumalis* cultivation.

## EXPERIMENTAL

### Materials

The strain *V. brumalis* was isolated, purified, and DNA testing was conducted in the Guizhou Institute of Biology, China (Li *et al*. 2022). This strain was activated using a specialized agar medium for *V. brumalis* and maintained at 15 °C. The agar medium composed of 10 g/L glucose, 10 g/L sucrose, 2 g/L beef extract, 1 g/L $K_2HPO_4$, 0.5 g/L $MgSO_4 \cdot 7H_2O$, 10 mg/L Vitamin $B_1$, 20 g/L agar powder, and 1 L deionized water mixture which was prepared by combining extracts obtained from boiling 200 g/L peeled potatoes, 40 g/L rice straw, and 50 g/L wheat bran separately for 30 min. The pH of the medium was adjusted to pH 8. The medium was sterilized in an autoclave (Boxun, YXQ-50G, Shanghai, China) at 121 °C for 20 min.

*Lignocellulosic materials*

All lignocellulosic materials were collected from Guiyang City, Guizhou Province, China. The materials included corn cobs, rice straw, *Quercus acutissima* sawdust, cottonseed hulls, corn stalks, wheat bran, rice bran, and pressed rapeseed residue. The substrates were chopped into small fragments, sun-dried, and then oven-dried at 60 °C. Some fragments were pulverized to a mesh size ranging between 40-mesh and 60-mesh using an electric grinder. Biological reagents, including lignin alkali, fermented soybean meal powder, and fermented corn pulp, were purchased from Beijing Solarbio Science & Technology Co., Ltd. (Beijing, China).

## Methods

*Liquid fermentation culture*

When the activated agar medium was fully covered by the mycelia of *V. brumalis*, five 5-mm diameter mycelial discs excised from the activated agar plates were transferred into a 250-mL Erlenmeyer flask, which was filled with 100 mL of liquid-state fermentation medium. The liquid-state fermentation medium were sterilized in the autoclave at 121 °C for 20 min, including 20.0 g/L glucose, 10.0 g/L fructose, 2.5 g/L soy protein, 2.5 g/L fermented corn pulp, 1 g/L $KH_2PO_4$, 0.5 g/L $K_2HPO_4$, 0.5 g/L $MgSO_4 \cdot 7H_2O$, and 10 mg/L vitamin $B_1$, was prepared with 1 L deionized water extracted from 200 g/L peeled potato. All Erlenmeyer flasks were incubated at 18 °C and shaken at 120 rpm for 15 days. After incubation the mycelial pellets in the Erlenmeyer flask were homogenized using a modular homogenizer HFJ-10 (Tianjin HengAo Technology Co., Ltd., China) at 5,000 rpm for 180 s. The mycelial pellets were used as inoculums.

The basic medium was taken as the experimental control (CK). The composition included 10 g/L glucose, 2 g/L $(NH_4)_2SO_4$, 0.5 g/L $MgSO_4 \cdot 7H_2O$, 0.46 g/L $KH_2PO_4$, 1 g/L $K_2HPO_4$. Transferred 0.3 g of primary cultivation substrates (corn cobs, rice straw, *Q. acutissima* sawdust, cottonseed hulls, or corn stalks) into a 250 mL Erlenmeyer flask, which had 100 mL of basic medium, as the induction medium with three replicates per treatment. Additionally, alkaline lignin was added as a comparative material with three replicates per treatment in the experiment to stimulate laccase secretion by *V. brumalis,* serving as a control for lignin degradation when used as the primary cultivation substrate. 0.3 g of auxiliary cultivation substrates (fermented soybean meal powder, fermented corn pulp, wheat bran, pressed rapeseed residue, or rice bran) were transferred into a 250-mL Erlenmeyer flask, which had 100 mL of basic medium, as the induction medium with three replicates per treatment. All Erlenmeyer flasks were sterilized in the autoclave at 121 °C for 30 min. After cooling, to each Erlenmeyer flask was added the 3 mL of homogenized inoculum. Afterwards all flasks were transferred into a rotary shaker (18 ℃, 120 rpm) for 16 days. The crude enzyme solution was extracted every two days. For each treatment, a 1 mL sample was taken each time.

*Assay of laccase activity*

The samples were centrifuged at a temperature of 4 ℃ with a rotational speed of 12,000 rpm for 20 min. Following centrifugation, the supernatants were stored at a temperature of -80 ℃ for subsequent analysis of the laccase activity.

The laccase activity was assayed with 2,2'-azinobis-[3-ethyltiazoline-6-sulfonate) (ABTS) (Han *et al*. 2022). The amount of enzyme required to convert 1 μmol of ABTS per minute was defined as one unit of enzyme activity. The molar extinction coefficient of ABTS at 420 nm is $3.6 \times 10^4 L/(mol \cdot cm)$.

*Effect on mycelial growth of solid-state fermentation culture*

Solid-state fermentation was conducted in the medium containing 10% wheat bran, 1% compound fertilizer (N-$P_2O_5$-$K_2O$=15-15-15)≅45%, 3% lime, and 86% agricultural and forestry wastes, which were different lignocellulosic materials including corn cob, rice straw, mixed sawdust from broad-leaved trees, cottonseed hull, or corn stalks. The mixed culture materials were divided into equal amounts and placed in a 350-mL original strain bottle (tissue culture bottle), and sterilized in the autoclave at 121 °C for 120 min. After cooling, an 8-mm punch was used to make circular plates along the edge of the colony. One plate was inoculated into one bottle. The plate was placed into the middle of the original strain bottle and incubated in an artificial climate chamber at 15 ℃ in the dark. Each original formula was repeated 18 times. The concentration of carbon dioxide was kept within 0.3%.

*V. brumalis* strains were cultured in the dark for 30 days for mycelial growth. The mycelial color was observed and recorded. The average daily mycelial growth rate (cm/d) = the length of mycelial extension from day 11 to day 20 of cultivation (cm) / 10 d.

*Data statistics*

Analyses of variance (ANOVA) between the test groups were performed with the PASW Statistics 18.0 (International Business Machines Corporation, 18.0, New York, NY, USA). The figures were created by WPS Office (Kingsoft, V12.1.0.16388, Beijing, China).

## RESULTS AND DISCUSSION

### Influence of Different Primary Cultivation Substrates on Laccase Activity in Liquid Fermentation of *V. brumalis*

As shown in Fig. 1, on the second day in cultivation, significant laccase activity was detected in all the added primary cultivation substrates. The laccase activity detected in the CK culture medium without any lignocellulosic inducers was significantly lower than that in the other inducing cultures (Fig. 1). This indicated that the addition with primary cultivation substrates could rapidly promote the laccase secretion of *V. brumalis* (Fig. 1). Under the induction of all primary cultivation substrates, the laccase activity of *V. brumalis* initially increased and then decreased as the cultivation time progresses (Fig. 1). Compared to the CK treatment, lignin alkali exhibited a stronger ability to stimulate laccase production in *V. brumalis* (Fig. 1). This confirmed that adding lignin alkali can induce fungi to produce more laccase (An *et al*. 2018; Han *et al.* 2020). Among several primary cultivation substrates, *Q. acutissima* sawdust stimulated the highest laccase activity in *V. brumalis*, successively followed by rice straw and corn stalks (Fig. 1). Cottonseed hulls and corn cobs could stimulate *V. brumalis* to reach the peak of the enzyme secretion earlier than *Q. acutissima* sawdust, rice straw, and corn stalks, but the maximum enzyme activities were significantly lower (Table 1 and Fig. 1). This indicated that *Q. acutissima* sawdust, corn stalks, and rice straw were more effective in stimulating *V. brumalis* to produce higher and more stable laccase activity than corn cobs and cottonseed hulls (Fig. 1).

The various lignocellulosic materials used in this study have been often employed to stimulate edible fungi to secrete laccase (Staji *et al.* 2006; Qin *et al.* 2017; An *et al*. 2020; Li *et al*. 2021; Xiong *et al*. 2021a). *Agaricus bisporus* grown on corn stalks produced more laccase than the one grown on weeds (Qin *et al.* 2017). The laccase production from *Pleurotus ostreatus* and *Flammulina velutipes* strains grown on cottonseed hull was higher

than that on corncob or poplar wood (An *et al*. 2020). The laccase vitality of *Auricularia cornea* '781' in the basal medium containing sawdust was lower than in the basal medium containing cottonseed hulls or corn cob ( Li *et al*. 2021). Corn cobs could stimulate *Lentinula edodes* 'L808' to produce more laccase than sawdust from *Coriaria nepalensis* or *Q. acutissima*, but the sawdust from *Coriaria nepalensis* could stimulate *L. edodes* 'Qianxingxun 1' to produce more laccase than corn cobs or the sawdust from *Q. acutissima* (Xiong *et al*. 2021a). Overall, cottonseed hulls and corn cobs were high-quality lignocellulosic materials effectively inducing laccase production in some edible mushrooms, such as *P. ostreatus*, *L. edodes*, *F. velutipes*, and *A. cornea*. (An *et al*. 2020, 2021; Li *et al*. 2021; Xiong *et al*. 2021a,b).

**Table 1.** Maximum Laccase Activity under Different Primary Cultivation Substrates Treatments, and Its Occurrence Time for *V. brumalis*

| Primary Cultivation Substrates | Maximum Laccase Viability (U/L) | Time (d) |
|---|---|---|
| CK | 32.87 | 6 |
| Lignin alkali | 47.38 | 6 |
| Corn cobs | 44.60 | 4 |
| Rice straw | 51.54 | 6 |
| *Q. acutissima* sawdust | 57.25 | 6 |
| Cottonseed hulls | 32.25 | 4 |
| Corn stalks | 50.77 | 6 |

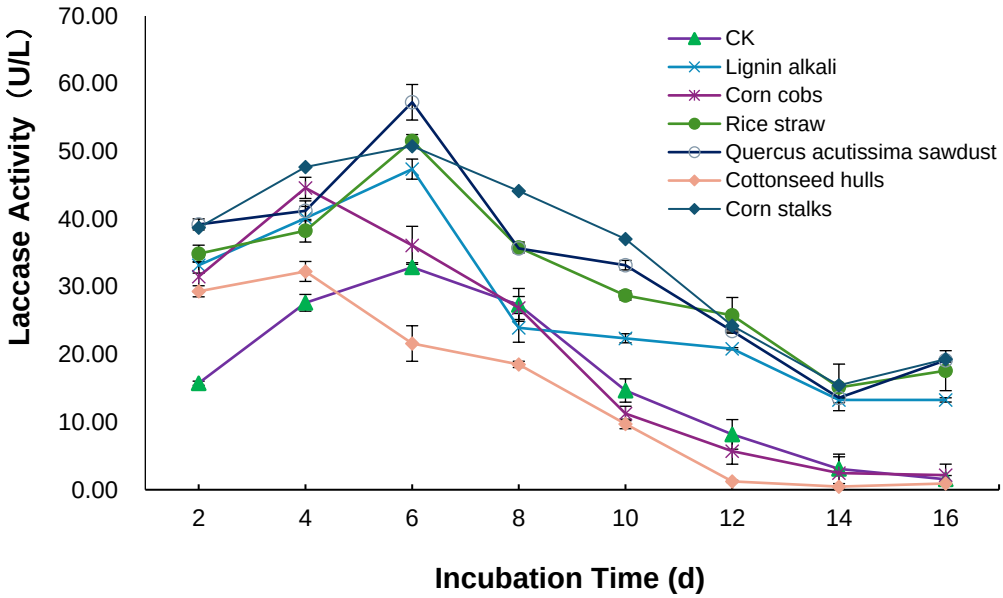


**Fig. 1.** The influence of different primary cultivation substrates on laccase activity in liquid fermentation of *V. brumalis*

## Influence of Different Auxiliary Cultivation Substrates on Laccase Activity in Liquid Fermentation of *V. brumalis*

As shown in Fig. 2, in all culturing media added with auxiliary cultivation substrates, the laccase activity exhibited a relatively consistent trend. However, there were significant differences of enzyme activity among the different inducers. Among several

auxiliary cultivation substrates, the highest enzyme production in *V. brumalis* was induced by wheat bran, in turn followed by pressed rapeseed residue (Table 2 and Fig. 2). Rice bran showed the lowest enzyme-inducing capability in *V. brumalis* (Table 2 and Fig. 2). Similarly, wheat bran demonstrated a significant inducing effect on laccase enzyme production of the other edible mushrooms (Atilano-Camino *et al*. 2020; Li *et al.* 2021). Rice bran stimulated the secretion of laccase for *L. edodes* 'Qianxiangxun 1' more strongly and persistently than wheat bran (Xiong *et al.* 2021b).

**Table 2.** Maximum Laccase Activity under Different Nitrogen Source Treatments, and Its Occurrence Time for *V. brumalis*

| Auxiliary Cultivation Substrates | Maximum Laccase Viability (U/L) | Time (d) |
|---|---|---|
| CK | 32.87 | 6 |
| Fermented soybean meal powder | 53.40 | 6 |
| Fermented corn pulp | 53.55 | 6 |
| Wheat bran | 65.12 | 6 |
| Pressed rapeseed residue | 55.40 | 6 |
| Rice bran | 45.06 | 6 |

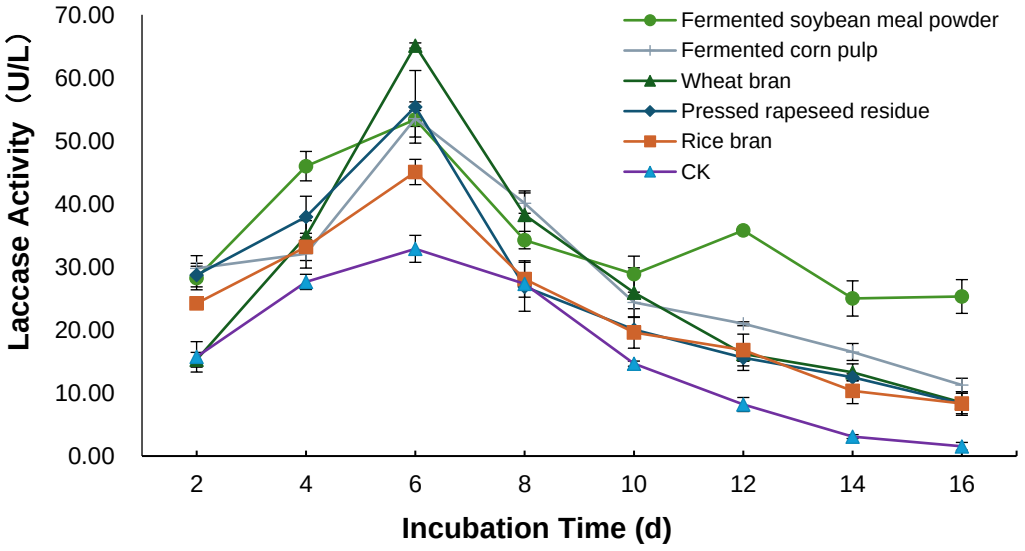


**Fig. 2.** The influence of different nitrogen sources on laccase activity in liquid fermentation of *V. brumalis*

## Effect of Different Lignocellulosic Materials on the Laccase Activity in Liquid Fermentation of *V. brumalis*

As shown in the one-way ANOVA in Table 3, the primary cultivation substrates had a highly significant impact on the laccase activity of *V. brumalis* during liquid submerged fermentation throughout the entire cultivation period ($P < 0.001$). The most profound effect occurred on the 6$^{th}$ day in the cultivation period, followed by the 12$^{th}$ day. The auxiliary cultivation substrates had a significant impact on the laccase activity of *V. brumalis* during liquid submerged fermentation ($P < 0.05$) (Table 3). The most pronounced effect occurred on the 12$^{th}$ day, followed by the 6$^{th}$ day, during the cultivation period. All

lignocellulosic inducers had a highly significant impact on the laccase activity of *V. brumalis* during liquid submerged fermentation ($P < 0.001$) (Table 3). The most pronounced effect occurred on the 6th day, followed by the 2nd day in the cultivation.

Both the trends of primary and auxiliary cultivation substrates on the laccase activity of *V. brumalis* were characterized with an initial increase followed by a decrease, with the activity being higher in the early stages of cultivation compared to the later stages (Figs. 1 and 2). The primary cultivation substrates could more rapidly stimulate *V. brumalis* to produce laccase than the auxiliary cultivation substrates, but the most auxiliary cultivation substrates exhibited higher potential and persistence in inducing laccase production in *V. brumalis* (Figs. 1 and 2). To improve quality and increase *V. brumalis* yield in commercial cultivation through stimulating *V. brumalis* to secrete more laccase, further research is needed for the components of primary and auxiliary cultivation substrates in the substrate formulation. Based on the results of this study, primary cultivation substrates, such as *Q. acutissima* sawdust, rice straw, corn stalks, and auxiliary cultivation substrates, such as wheat bran and pressed rapeseed residue, should be given priority in consideration for cultivating *V. brumalis*.

In the cultivation history of straw mushrooms, agricultural and forestry waste, such as rice straw, cottonseed hulls, mixed wood chips, wheat bran, and rice bran, had been commonly used as primary or supplementary cultivation materials (Luo and Chen 2010). Rice bran had shown a relatively low ability to stimulate laccase production in *V. brumalis* in this study and would not be considered in the subsequent validation experiments (Fig. 2). Therefore, *Q. acutissima* sawdust, rice straw, cottonseed hulls, corn cobs, and corn stalks were used as the primary cultivation substrates, respectively, and wheat bran was used as an auxiliary material for the solid-state fermentation cultivation of *V. brumalis* in the subsequent experiments.

**Table 3.** Effect of Different Lignocellulose on Laccase Activity in Liquid Fermentation of *V. brumalis* by One-way ANOVA

| Incubation Time (d) | Primary Cultivation Substrates (U/L) | Auxiliary Cultivation Substrates (U/L) | All Lignocellulose (U/L) |
|---|---|---|---|
| 2 | 189.179*** | 130.368*** | 318.878*** |
| 4 | 144.073*** | 117.085** | 75.834*** |
| 6 | 481.005*** | 237.222*** | 426.762*** |
| 8 | 225.389*** | 103.643* | 169.449*** |
| 10 | 297.339*** | 78.686** | 184.673*** |
| 12 | 310.864*** | 256.54*** | 271.779*** |
| 14 | 135.633*** | 156.509*** | 143.436*** |
| 16 | 225.569*** | 188.113*** | 184.574*** |
| Note: df = 6;*P < 0.05,**P < 0.01,***P < 0.001 | | | |

## Effect of Different Primary Cultivation Substrates on the Mycelial Growth of *V. Brumalis* in Solid-State Fermentation

From Table 4 and Fig. 3, *V. brumalis* could grow well on the media with different culturing formulas, but the mycelial growth rates showed differences at the $P < 0.05$ level. In the medium with formulation 2, the mycelial grew the fastest relative to the other media, with a growth rate of 0.32 cm/d, followed by the medium with formulation 3.

**Table 4.** Effect of Different Primary Cultivation Substrates on the Mycelial Growth of *V. brumalis* under Solid-State Fermentation

| Serial Number | Cultivation primary Substrate | Average Daily Mycelial Growth Rate (cm/d) | Mycelial Growth | Morphological Description |
|---|---|---|---|---|
| 1 | Corn cobs | 0.19 ± 0.01 c | ++ | The mycelia were grayish white, relatively dense, and grew slowly, with yellow pigment. |
| 2 | Rice straw | 0.32 ± 0.02 a | + | The mycelia were grayish white, thin, and grew quickly without yellow pigment. After colonization, the mycelia became denser. |
| 3 | *Q. acutissima* sawdust | 0.29 ± 0.03 ab | +++ | The mycelia were grayish white, dense, and grew quickly without yellow pigment. |
| 4 | Cottonseed hulls | 0.22 ± 0.01 bc | ++ | The mycelia were grayish white, relatively dense, and grew relatively slowly, with yellow pigment. |
| 5 | Corn stalks | 0.25 ± 0.02 bc | ++ | The mycelia were grayish white, relatively dense, and grew relatively quickly without yellow pigment. |

Note: The data in the table are presented as mean ± standard error (n = 18). Different lowercase letters indicate significant differences between groups ($P < 0.05$), while the same letters indicate no significant difference ($P > 0.05$). The "+" sign indicates the mycelial growth. The more "+" signs there are, the stronger the mycelial growth and the higher the density.


**Fig. 3.** The effect of different primary cultivation substrates on the mycelial growth of *V. brumalis* in solid-state fermentation: a: Formulation 1, b: Formulation 2, c: Formulation 3, d: Formulation 4, and e: Formulation 5

In the medium using the formulation 3, *V. brumalis* colony grew the densest compared to the other formulas. The mycelia grew slowly on the medium using formulations 1 and 4. Considering both mycelial growth vigor and growth speed, the medium using formulation 3 (*Q. acutissima* sawdust) was most suitable for the mycelial growth, followed by the medium using formulation 2 (rice straw). This indicated that *V. brumalis* could grow well in the substrates primarily composed of *Q. acutissima* sawdust or rice straw (Table 3). This is somewhat similar to the growth behavior of *V. bombycina*

(Chen and Luo 2018). But the field cultivation of *V. brumalis* to test the new formulation mentioned above is needed to verify whether it can achieve the intended yield increase.

## CONCLUSIONS

1. Wheat bran and pressed rapeseed residue stimulated *V. brumalis* to produce more laccase than soybean meal powder, fermented corn pulp, and rice bran.
2. *Q. acutissima* sawdust and rice straw were more favorable over corn stalks, cottonseed hulls, and corn cobs for laccase production and mycelial growth.
3. To improve quality and quantity of *V. brumalis* in commercial cultivation through stimulating *V. brumalis* to secrete more laccase, *Q. acutissima* sawdust , rice straw, and wheat bran should be given priority in consideration of the cultivating materials to farm *V. brumalis*.

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