Effect of Different Lignocellulosic Biomasses on Laccase Production by *Pleurotus* Species

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The laccase activity of three cultivated *Pleurotus* strains was investigated using different lignocellulosic biomasses for solid-state fermentation. The lignocellulosic biomasses were *Sophora japonica*, *Salix babylonica*, *Populus beijingensis*, and *Pinus tabuliformis*, which were selected because of their laccase producing ability and low cost. The maximum laccase activities from *P. ostreatus* Han 1189, *P. citrinopileatus* Han 1192, and *P. eryngii* Han 1205 using *Sophora japonica* were 768.74 U/L ± 11.25 U/L, 144.77 U/L ± 9.70 U/L, and 200.42 U/L ± 6.85 U/L, respectively. The three species of *Pleurotus* showed consistency in having a preference of hardwood to secret laccase under solid-state fermentation when facing hardwood and softwood as substrates. Furthermore, the presence of *Sophora japonica* was beneficial to improving the laccase activity for three *Pleurotus* strains. The capacity of the laccase secretion of *P. ostreatus* Han 1189 was superior to the capacity of *P. citrinopileatus* Han 1192 and *P. eryngii* Han 1205. The discovery was helpful for obtaining new high-producing strains and suitable wood materials, as well as expanding these high-producing strains for industrial applications to obtain high laccase activity, high laccase yield, and low cost laccase.

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INTRODUCTION

Currently, the primary sources (80% to 88%) of the world energy supply are fossil fuels, *e.g.*, crude oil, coal, and natural gas, which are non-renewable, limited, and costly (Erakhrumen 2014; Taha *et al*. 2015). Meanwhile, the demand for and amount consumed of energy is still rising, as it is necessity for human life (Yousef *et al*. 2021a,b). Using fossil fuels, *e.g.*, gasoline, as a primary source of energy has environmental impacts, including air, water, and soil pollution, as well as negative effects on public health (Galbe and Zacchi 2002; Taha *et al*. 2015). The methods of obtaining sustainable bioenergy from biomaterials, *e.g.*, bioethanol, not only can reduce reliance on fossil fuels, but the final product may also have a greater economical and net performance. As such, lignocellulosic biomass, the most abundant renewable material on earth, has attracted considerable attention because of its ability to be converted into other products (Kumar *et al*. 2016; Gaikwad and Meshram 2020; An *et al*. 2021c; Galic *et al.* 2021; Han *et al*. 2021b). Fungi cultured with lignocellulosic biomass can produce fruiting bodies for sale or eating and produce various other products,

e.g., enzymes and sterol. Furthermore, numerous enzymes related to lignocellulosic degradation could be secreted by these fungi, *e.g.*, ligninolytic enzymes, cellulase, and hemicellulose. Among the ligninolytic enzymes, laccase, as a long since discovered enzyme, has been widely studied in different research fields.

Laccase (EC 1.10.3.2), also called *p*-diphenol or dioxygen oxidoreductase, was first described in *Toxicodendron vernicifluum*, which was primitively named *Rhus vernicifera*; it was subsequently found in bacteria, fungi, and some insects (Zerva *et al*. 2019; Kumar *et al.* 2021; Khatami *et al*. 2022). Laccase displays a wide substrate specificity, along with the simultaneous reduction of molecular oxygen to water (Garrido-Bazán *et al*. 2016; Hernández *et al*. 2017). Based on this, laccase could be applied in many fields related to biotechnology, environmental protection, and medicine, *e.g.*, lignin degradation, biocatalysis, bioremediation and detoxification, food and beverages, detergents, sensors and biofuel cells, biopolymers, nanobiotechnology, and biomedicine (Baldrian 2006; Kunamneni *et al*. 2008; Chauhan *et al*. 2017; Mate and Alcalde 2017; Yang *et al*. 2017; Agrawal *et al*. 2018; Munk *et al*. 2018; Navas *et al*. 2019; Unuofin *et al*. 2019; Zerva *et al*. 2019; Xu *et al*. 2020). However, the widespread application of laccase in numerous aspects of biotechnological processes has been limited due to low laccase activity, low laccase yields, and the high laccase costs (Cardona *et al*. 2010; Wang *et al*. 2019). Effective laccase production strategies have attracted increasing research attention to improve activity and reduce cost (Akpinar and Urek 2017; Chenthamarakshan *et al*. 2017).

Currently, laccase is primarily secreted by bacteria and fungi. Laccase products are primarily higher-plant laccase and fungal laccase. Producing laccase *via* fungi is primarily concentrated in white-rot fungi of the *Aspergillus* and *Trichoderma* genus. This is likely because the laccase production is highest in white-rot fungi. Fungal species are also important factors affecting enzyme activity. Therefore, it is meaningful to develop a new enzyme-producing strain belonging to white rot fungi. Another important factor affecting enzyme activity is the fermentation method. At present, the primary fermentation methods include submerged fermentation, solid-state fermentation, and solid fermentation combined with submerged fermentation (An *et al*. 2016; Dey *et al*. 2016). Previously, submerged fermentation (SF) has been the most common approach for producing most enzymes, including laccase. Submerged fermentation provides a uniform distribution of nutrients, allowing adequate exposure and absorption of nutrients by cultured microorganisms. However, the disadvantage of SF is higher energy consumption. Under this circumstance, there has been a trend towards an increasing use of solid state fermentation (SSF) to produce certain enzymes over the past decade (Xin and Geng 2011; Nguyen *et al*. 2018; An *et al*. 2021a; An *et al*. 2021b; Liu *et al*. 2022). Compared with SF, the desired microorganism grown on solid lignocellulosic biomass with the absence of free water is closer to their natural environment in the wild (Jaramillo *et al*. 2017). In addition, being a simpler operating technique, there is lower energy consumption and lower dilution of the enzymes, which are the major advantages of SSF. Lignocellulosic biomass is the commonly substrate used for fungi growth. The selection of different types of lignocellulosic materials and the optimization of the media are the methods that many research groups have used to improve laccase activity (Tisma *et al*. 2012; Soumya *et al*. 2016).

Previous research had studied laccase secreted by numerous fungi cultivated on lignocellulosic biomass, *e.g.*, *Coriolopsis gallica* on sawdust waste, and *Ganoderma lucidum* on rice husks, rice straw, and sunflower seed hulls (Daâssi *et al*. 2016; Postemsky *et al*. 2017; Zhang *et al*. 2018). In addition, many studies indicated that *Pleurotus ostreatus*

is also an excellent producer of laccase (Karp *et al*. 2015; An *et al*. 2018; Brugnari *et al*. 2018; Song *et al*. 2020; Perez-Montiel *et al*. 2021; Cruz-Vazquez *et al*. 2022; Duran-Sequeda *et al*. 2022). Under these circumstances, it is important to evaluate the laccase-producing ability of different species belonging to the *Pleurotus* genus for developing new strains for enzyme production. In the present study, the laccase activities of three cultivated *Pleurotus* sp. strains, grown on lignocellulosic biomass, were reported. The lignocellulosic biomass used was all wood materials with a high lignin content. The results were helpful for obtaining new high-producing strains and suitable wood materials, as well as expanding high-producing strain for industrial application to obtain high laccase activity, high laccase yield, and low cost laccase.

EXPERIMENTAL

Materials

Microorganisms

Three cultivated strains, Han 1189, Han 1192, and Han 1205, from the genus of *Pleurotus*, were purchased from a local market in China (Langfang city, Hebei province, China). All strains were isolated and purified on complete yeast medium (CYM) and maintained at the college of life science, Langfang Normal University.

Lignocellulosic biomass

Four different lignocellulosic biomasses (*Sophora japonica*, *Salix babylonica*, *Populus beijingensis*, and *Pinus tabuliformis*) were collected from Langfang city, then cut into small pieces, and air-dried. All the small pieces of lignocellulosic biomass were subjected to grinding and milling to a fine powder with a particle size between 20- and 60-mesh using a FZ102 micro plant grinding machine (Tianjin Taisite Instrument Co., Ltd.). These were kept in a dry environment for further use as the nutrient substance for fungi growth and crude enzyme induction.

Methods

Fungal culture and inoculums preparation

To perform the activation of the fungus, three cultivated *Pleurotus* strains were transferred and grown on new CYM agar plates at a temperature of 26 °C for 7 d. Five 5-mm fungal mycelium disks, which were excised from the CYM agar plates, were transferred into 250 mL flasks containing 100 mL of malt extract agar (MEA) liquid medium. All flasks were maintained in a rotary shaker at 150 rpm at a temperature of 26 °C. Mycelial pellets were harvested after 7 d and mixed with a laboratory blender (Ningbo Xinzhi Biotechnology Co., Ltd.) for 2 min at 8000 rpm. These suspensions would act as the inoculum.

Induction laccase production of fungi

First, 2 g of the milled lignocellulosic biomass was moistened with 10 mL of basal solution ($MgSO_4 \cdot 7H_2O$ 0.5 g/L, K_2HPO_4 1 g/L, and KH_2PO_4 0.46 g/L) in a 250 mL Erlenmeyer flasks and autoclaved at a temperature of 121 °C for 30 min. After cooling, 3 mL of inoculum was added into the flasks and all cultivations were carried out at a temperature of 26 °C while undergoing agitation (at 150 rpm).

Enzyme activity

First, 100 mL of acetate-sodium acetate buffer (50 mM, at a pH of 5.5) was added into each of the flasks containing a fermentation substrate at different time intervals. Then, these flasks were transferred into a rotary shaker to perform the extraction (at a temperature of 10 °C, at 120 rpm, for 4 h) (An *et al.* 2021a). To determine the extracellular laccase activities, the lignocellulosic biomass and mycelium soaked into the culture fluid were removed *via* filter paper, and the filtered liquid was centrifuged (at 12000 rpm for 15 min at a temperature of 4 °C). The supernatant obtained after centrifugation was preserved at a temperature of -80 °C and used for subsequent determination of the laccase activity.

The laccase activity was assayed with 2,2'-azinobis-[3-ethyltiazoline-6-sulfonate] (ABTS) as the substrate, which was referred to the description previously by Han *et al*. (2021b). The assay mixture (300 µL) was prepared with 190 µL of 50 mM acetate-sodium acetate buffer (a pH of 4.2), 100 µL of 1 mM ABTS, and 10 µL of the appropriately diluted enzyme sample. Then, the reaction mixture was measured using an iMark^{TM} microplate absorbance reader (Bio-Rad, Hercules, CA). For calculating the laccase activity molar extinction coefficient of the oxidized ABTS at 415 nm, $\mathcal{E} = 3.16 \times 10^4$ M^{-1} cm^{-1}, was used. The laccase activity was expressed in Units, where one unit was defined as the amount of laccase required to oxidize 1 µmol of ABTS per min.

Statistical analysis

Analyses of variance (ANOVA) between the fungi and lignocellulosic biomass were performed using the SPSS statistical program. The colored figures were created by Origin 2016.

Nucleic acid (fungal DNA) extraction and PCR amplification

Genomic DNA of three *Pleurotus* strains was collected using a cetyltrimethyl-ammonium bromide (CTAB) rapid plant genome extraction kit-DN14. The method for obtaining the mycelium was outlined in Han *et al*. (2016) and Han *et al.* (2021a). In addition, ITS1 and ITS4 primers (for Han 1192) and ITS5 and ITS4 primers (for Han 1189 and Han 1205) were used for PCR amplification in a thermocycler (Applied Biosystems, Waltham, MA) (White *et al.* 1990). The PCR products were detected *via* electrophoresis, and the qualified products were sent to Beijing Genomics Institute (Beijing, China) for sequencing. The sequenced data was edited and processed using BioEdit software, and then blasted and identified on the National Centre for Biotechnology Information website (NCBI, http://www.ncbi.nlm.gov/). Finally, these new internal transcribed spacer (ITS) sequences of Han 1189, Han 1192, and Han 1205 were submitted to the GenBank website, and the GenBank numbers were ON197668, ON197669, and ON197670, respectively.

RESULTS AND DISCUSSION

Identification of the Three Cultivated *Pleurotus* Strains

The taxonomic status of strains Han 1189, Han 1192, and Han 1205, as identified *via* ITS sequence, were *Pleurotus ostreatus*, *Pleurotus citrinopileatus*, and *Pleurotus eryngii*, respectively.

Results of the Statistical Analysis

The fungi and lignocellulosic biomass significantly affected the laccase activity (*p*-value less than 0.001) at different times of cultivation (Table 2). Meanwhile, the interaction of the fungi and lignocellulosic biomass significantly affected the laccase activity during the whole fermentation process (*p*-value less than 0.001) (Table 2).

Table 1. Effects of the Fungi, Lignocellulosic Biomass, and the Interactions of Fungi and Lignocellulosic Biomass on Laccase Activity (Two-way ANOVA)

Incubation Period (d)	Fungi	Lignocellulosic Biomass	Fungi × Lignocellulosic Biomass
1	339.785***	287.573***	173.724***
2	459.189***	1199.281***	325.173***
3	254.580***	976.017***	334.407***
4	567.181***	643.613***	686.586***
5	10445.916***	12104.754***	12286.544***
6	837.171***	734.406***	882.014***
7	4958.966***	2656.169***	2497.692***
8	925.860***	906.263***	208.682***
9	975.725***	2006.693***	693.179***
10	259.675***	305.456***	333.522***
Note: df = 2, 3, 6; ****p*-value less than 0.001			

Effect of Various Lignocellulosic Biomasses on Laccase Activity

Microorganisms capable of degrading lignins usually secrete extracellular lignin-degrading enzymes (Martani *et al*. 2017). Lignocellulosic biomass is a valuable substrate for laccase production. Abundant studies have provided evidence that lignins can stimulate laccase production (Liu *et al*. 2013; Adekunle *et al*. 2017; Mishra *et al*. 2017; Palazzolo *et al*. 2019; Liu *et al*. 2022). However, selecting a suitable lignocellulose to stimulate laccase production by fungi will be one of the important methods for efficient laccase production using solid state fermentation (Elisashvili *et al*. 2008; An *et al*. 2021a,c; Han *et al*. 2021b).

At the beginning of the fermentation process, the laccase activities of *Pleurotus ostreatus* Han 1189 with *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* were 5.83 U/L ± 0.70 U/L, 27.93 U/L ± 2.01 U/L, 16.38 U/L ± 0.92 U/L, and 14.67 U/L ± 0.17 U/L, respectively (as shown in Fig. 1). Interestingly, the laccase activity detected in broad-leaved trees (*Sophora japonica*, *Salix babylonica*, and *Populus beijingensis*) was higher than the laccase activity in coniferous trees (*Pinus tabuliformis*). Therefore, *Sophora japonica* may be a suitable lignocellulosic biomass for stimulating *P. ostreatus* Han 1189 to secret laccase due to the laccase activity detected at the 1st day. The maximum laccase activity of *P. ostreatus* Han 1189 with *Sophora japonica* was 768.74 U/L ± 11.25 U/L on the 7th day, nearly 8.25-fold, 4.67-fold, and 3.82-fold higher than the laccase activity of *Pinus tabuliformis* (93.13 U/L ± 3.65 U/L, 6th day), *Salix babylonica* (164.46 U/L ± 3.32 U/L, 8th day), and *Populus beijingensis* (201.13 U/L ± 16.92 U/L, 8th day) (as shown in Table 2). Clearly, broad-leaved trees were more helpful for *P. ostreatus* Han 1189 in terms of improving laccase activity. However, the laccase activity detected on

10th day was 308.12 U/L ± 28.43 U/L, which was approximately 7.82-fold, 513.53-fold, and 34.08-fold higher than the laccase activity of *Pinus tabuliformis* (39.38 U/L ± 0.92 U/L), *Salix babylonica* (0.60 U/L ± 0 U/L), and *Populus beijingensis* (9.04 U/L ± 1.09 U/L) (Fig. 1). Furthermore, the laccase activity value of *Sophora japonica* was greater than 300 U/L from the 3rd day to the 10th day of fermentation (Fig. 1). This seems to indicate that a relatively stable and continuous laccase activity can be obtained with this lignocellulosic biomass. Obviously, broad-leaved trees, especially *Sophora japonica*, were more suitable for *Pleurotus ostreatus* Han 1189 in terms of secreting laccase.

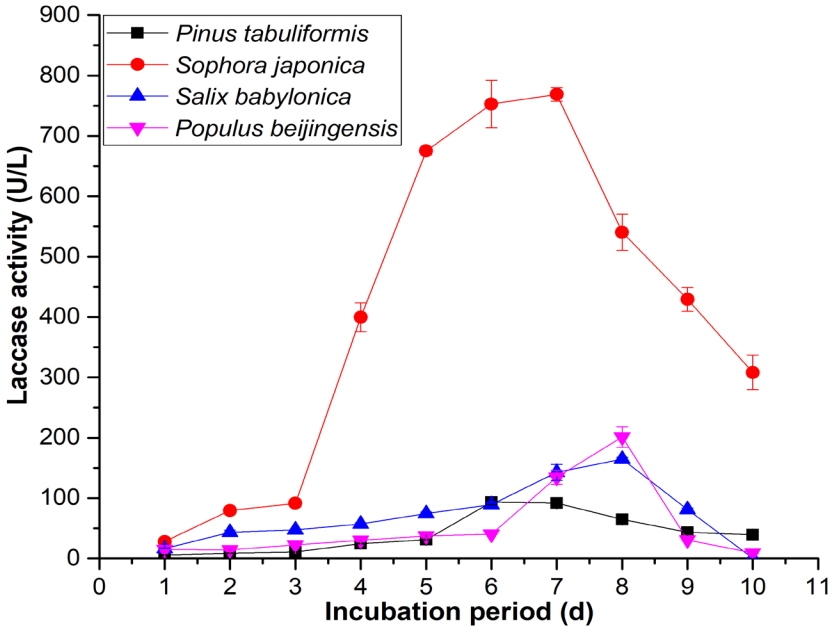

Fig. 1. Laccase activity of *Pleurotus ostreatus* Han 1189 grown on *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* using solid-state fermentation

Table 2. Maximum Laccase Activity, Lignocellulosic Biomass, and Occurrence Time of Cultivated *Pleurotus* sp. Strains

Maximum Laccase Activity (U/L)	Lignocellulosic Biomass	Fungi	Time (d)
93.13 ± 3.65	*Pinus tabuliformis*	*Pleurotus ostreatus* Han 1189	6th
768.74 ± 11.25	*Sophora japonica*	*Pleurotus ostreatus* Han 1189	7th
164.46 ± 3.32	*Salix babylonica*	*Pleurotus ostreatus* Han 1189	8th
201.13 ± 16.92	*Populus beijingensis*	*Pleurotus ostreatus* Han 1189	8th
33.35 ± 1.52	*Pinus tabuliformis*	*Pleurotus citrinopileatus* Han 1192	7th
144.77 ± 9.70	*Sophora japonica*	*Pleurotus citrinopileatus* Han 1192	8th
102.57 ± 3.47	*Salix babylonica*	*Pleurotus citrinopileatus* Han 1192	5th
134.82 ± 5.39	*Populus beijingensis*	*Pleurotus citrinopileatus* Han 1192	8th
38.18 ± 1.66	*Pinus tabuliformis*	*Pleurotus eryngii* Han 1205	5th
200.42 ± 6.85	*Sophora japonica*	*Pleurotus eryngii* Han 1205	9th
130.30 ± 8.79	*Salix babylonica*	*Pleurotus eryngii* Han 1205	6th
117.54 ± 4.35	*Populus beijingensis*	*Pleurotus eryngii* Han 1205	6th
Note: the data is presented as the mean ± standard deviation for biological triplicates and is expressed as U/L			

For the 1st day, the laccase activity value from *Pleurotus citrinopileatus* Han 1192 could be measured for *Pinus tabuliformis* (4.32 U/L ± 0.17 U/L), *Salix babylonica* (14.37 U/L ± 0.35 U/L), and *Populus beijingensis* (10.95 U/L ± 0.97 U/L), and unmeasured on *Sophora japonica* (Fig. 2). The maximum laccase activity from *P. citrinopileatus* Han 1192 was 33.35 U/L ± 1.52 U/L (7th day), 144.77 U/L ± 9.70 U/L (8th day), 102.57 U/L ± 3.47 U/L (5th day), and 134.82 U/L ± 5.39 U/L (8th day) for *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis*, respectively (Table 2). In other words, the maximum laccase activity for *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* was approximately 4.34-fold, 3.08-fold, and 4.04-fold higher than the laccase activity for *Pinus tabuliformis*. However, broad-leaved trees were more conducive to the secretion of laccase for *P. citrinopileatus* Han 1192. Interestingly, the highest laccase activity of the tested four lignocellulosic biomasses was still present for *Sophora japonica*, although no laccase activity was detected for *Sophora japonica* at the 1st day. In addition, the laccase activity level from *P. citrinopileatus* Han 1192 with *Pinus tabuliformis* was low throughout the whole fermentation stage.

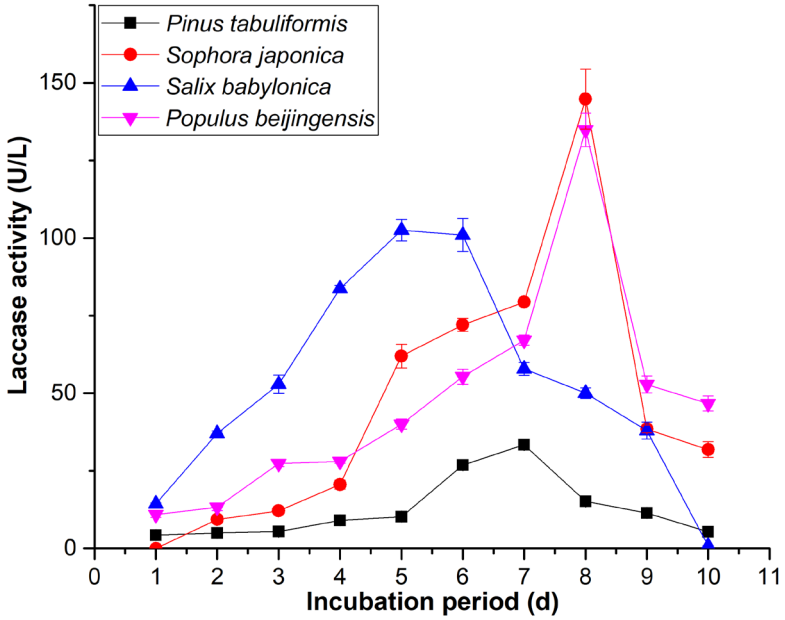

Fig. 2. Laccase activity of *Pleurotus citrinopileatus* Han 1192 grown on *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* using solid-state fermentation

On the 1st day, the laccase activity of *Pleurotus eryngii* Han 1205 for *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* was 2.91 U/L ± 0.17 U/L, 10.95 U/L ± 0.87 U/L, 15.47 U/L ± 0.76 U/L, and 11.05 U/L ± 0.87 U/L, respectively (as shown in Fig. 3). Therefore, the laccase activity for *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* was approximately 3.76-fold, 5.32-fold, and 3.80-fold greater than *Pinus tabuliformis*, respectively. The maximum laccase activities value for *P. eryngii* Han 1205 with *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* were 38.18 U/L ± 1.66 U/L, 200.42 U/L ± 6.85 U/L, 130.30 U/L ± 8.79 U/L, and 117.54 U/L ± 4.35 U/L, respectively, and its time of occurrence was the 5th day, 9th day, 6th day, and 6th day, respectively (as shown in Table 2). In conclusion, the maximum laccase activity of *P. eryngii* Han 1205 using *Sophora japonica*, *Salix babylonica*, and *Populus beijingensis* was approximately 5.25-fold, 3.41-fold, and 3.08-fold higher than the laccase activity for *Pinus tabuliformis*. As such, it was not hard to see that broad-leaved trees were more useful for *P. eryngii* Han 1205 in terms of secreting laccase. Furthermore, *Sophora japonica* was beneficial for *P. eryngii* Han 1205 in terms of secreting laccase.

Previous studies indicated that laccase activity may be adversely affected by an excessive lignin content. Gómez *et al*. (2005) found that the laccase activity from cultures with barley bran (1799.6 U/L) was approximately 2-fold higher than the laccase activity from cultures with chestnut shell (959.8 U/L). Chen *et al*. (2011) evaluated the laccase activity from seven plant species under solid-state fermentation and observed maximal laccase activity (10,700 IU/g) in cultures with rice straw (lignin 10% to 15% w/w). In addition, the tested lignocellulosic biomass belonged to hardwood stems (*Sophora japonica*, *Salix babylonica*, and *Populus beijingensis*) and softwood stems (*Pinus tabuliformis*). The lignin content of hardwood stems is 18% to 25%, while the lignin content of softwood stems is 25% to 35% (Malherbe and Cloete 2002; Howard *et al*. 2003; Sánchez 2009). As such, the present study also indicated that excessive lignin content was

a disadvantage in terms of fungi secreting laccase, because the laccase activity from hardwood stems was higher than the laccase activity from softwood stems. Han *et al*. (2021b) found that maximum laccase activity of *Cerrena unicolor* Han 849, *Lenzites betulina* Han 851, and *Schizophyllum commune* Han 881 with *Firmiana platanifolia* was 552.34 U/L ± 49.14 U/L, 309.72 U/L ± 12.53 U/L and 5.22 U/L ± 0.35 U/L, which was higher than the laccase activity for *Pinus tabuliformis* (223.53 U/L ± 21.06 U/L, 36.57 U/L ± 3.39 U/L, and 1.51 U/L ± 0.00 U/L), respectively. A similar phenomenon appeared in this study. An *et al*. (2021a) indicated that the presence of cottonseed hull and *Populus beijingensis* were useful for improving the laccase activity of *P. ostreatus* CY 568. However, this study found that the presence of *Sophora japonica* was more beneficial in terms of enhancing the laccase activity than *Populus beijingensis*. In conclusion, broad-leaved trees, especially *Sophora japonica*, were more suitable for the three cultivated strains of *Pleurotus* in terms of secreting laccase.

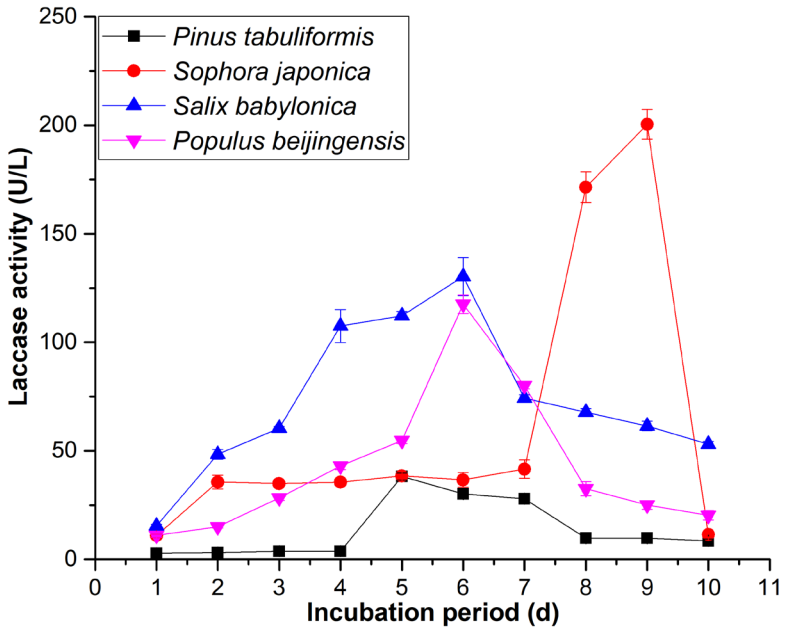

Fig. 3. Laccase activity of *Pleurotus eryngii* Han 1205 grown on *Pinus tabuliformis*, *Sophora japonica*, *Salix babylonica,* and *Populus beijingensis* using solid-state fermentation

Effect of Different Fungi on Laccase Activity

Numerous studies have sought to find new high-laccase producing strains (Chen *et al*. 2011; Xu *et al*. 2016; Sun *et al*. 2020; Han *et al*. 2021b; Khatami *et al*. 2022). Generally, screening laccase-producing strains focuses on three primary methods, *i.e.*, different species with far different taxonomic status, different species belonging to one genus, and different strains from one species. Janusz *et al*. (2015) studied the laccase activity of various strains of *Flammulina velutipes* and found that the laccase producing ability of the different strains was considerably different. Huang *et al*. (2019) analyzed the ability of a number of edible fungi to degrade crop straw and found that different edible fungi had different abilities to secrete enzymes. As such, developing new laccase producing strains is still one of the important methods for producing high levels of low-cost laccase.

In terms of the laccase activity of *Pinus tabuliformis*, the laccase activities from *Pleurotus ostreatus* Han 1189, *P. citrinopileatus* Han 1192, and *P. eryngii* Han 1205 were

5.83 U/L ± 0.70 U/L, 4.32 U/L ± 0.17 U/L and 2.91 U/L ± 0.17 U/L on the 1st day (as shown in Fig. 1 through Fig. 3). On the 1st day, the laccase activities of *P. ostreatus* Han 1189, *P. citrinopileatus* Han 1192, and *P. eryngii* Han 1205 with *Sophora japonica* were 27.93 U/L ± 2.01 U/L, 0 U/L ± 0 U/L and 10.95 U/L ± 0.87 U/L, respectively. Obviously, the laccase activity of *P. ostreatus* Han 1189 with *Pinus tabuliformis* or *Sophora japonica* was higher than the laccase activity of *P. citrinopileatus* Han 1192 or *P. eryngii* Han 1205. Similarly, the same phenomenon occurred when *Salix babylonica* was used as a substrate (as shown in Fig. 1 through Fig. 3). The laccase activity of *P. ostreatus* Han 1189 was lower than the laccase activity of the other two species when *Populus beijingensis* was used as a substrate.

The maximum laccase activity values of *P. ostreatus* Han 1189, *P. citrinopileatus* Han 1192, and *P. eryngii* Han 1205 with *Pinus tabuliformis* were 93.13 U/L ± 3.65 U/L, 33.35 U/L ± 1.52 U/L, and 38.18 U/L ± 1.66 U/L, respectively (Table 2). Therefore, the maximum laccase activity of *P. ostreatus* Han 1189 was approximately 2.79-fold and 2.44-fold higher than the laccase activities of *P. citrinopileatus* Han 1192 and *P. eryngii* Han 1205, respectively. Similarly, the maximum laccase activity values for *P. ostreatus* Han 1189 with *Sophora japonica* was 768.74 ± 11.25 U/L, which was approximately 5.31-fold and 3.84-fold higher than the laccase activities of *P. citrinopileatus* Han 1192 (144.77 U/L ± 9.70 U/L) and *P. eryngii* Han 1205 (200.42 U/L ± 6.85 U/L), respectively. Furthermore, the laccase activity of *P. ostreatus* Han 1189 from day 3 to day 10 of fermentation was higher than the maximum laccase value of *P. citrinopileatus* Han 1192 and *P. eryngii* Han 1205. This also reflected that *P. ostreatus* Han 1189 had the advantages of stable laccase production and high activity compared to *P. citrinopileatus* Han 1192 and *P. eryngii* Han 1205. The maximum laccase activities of *P. ostreatus* Han 1189 with *Salix babylonica* and *Populus beijingensis* were 164.46 U/L ± 3.32 U/L and 201.13 U/L ± 16.92 U/L, respectively, which were greater than the laccase activities of *P. citrinopileatus* Han 1192 (102.57 U/L ± 3.47 U/L and 134.82 U/L ± 5.39 U/L) and *P. eryngii* Han 1205 (130.30 U/L ± 8.79 U/L and 117.54 U/L ± 4.35 U/L), respectively. Therefore, the laccase secretion of *P. ostreatus* Han 1189 was greater than the secretions from *P. citrinopileatus* Han 1192 and *P. eryngii* Han 1205.

The laccase activities of *Pleurotus ostreatus* IBB 8, *P. ostreatus* 2175, and *P. tuberregium* IBB 624 were 7 ± 0.7 or 7 U/flask ± 0.8 U/flask, 15 ± 1.4 or 12 U/flask ± 1.2 U/flask, ands 20 ± 1.8 or 10 U/flask ± 1.0 U/flask, respectively, when grown on tree leaves or wheat straw (Elisashvili *et al*. 2008). An *et al*. (2020) found that the laccase activity of *P. ostreatus* CCEF 89 was 748.24 U/L ± 9.53 U/L, 699.12 U/L ± 44.91 U/L, and 509.75 U/L ± 15.43 U/L using submerged fermentation with cottonseed hull, corncob, and poplar wood, respectively. The laccase activity of *P. ostreatus* CY 568 and *P. ostreatus* CCEF 99 for sawdust and corncob was 353.83 U/L ± 11.94 U/L and 440.73 U/L ± 8.36 U/L, and 548.72 U/L ± 19.59 U/L and 286.12 U/L ± 25.80 U/L, respectively, when using solid-state fermentation (Han *et al*. 2020). Therefore, the laccase secretion ability of *P. ostreatus* Han 1189 was better than the other *P. ostreatus* strains in previous studies.

CONCLUSIONS

1. Three cultivated strains, belonging to the *Pleurotus* genus, showed a uniform preference for hardwood in terms of secreting laccase under solid-state fermentation conditions when facing hardwood and softwood as substrates.

2. The presence of *Sophora japonica* was beneficial in terms of improving the laccase activity for *Pleurotus ostreatus* Han 1189, *Pleurotus citrinopileatus* Han 1192, and *Pleurotus eryngii* Han 1205.
3. The laccase secretion capacity of *P. ostreatus* Han 1189 was superior to the laccase secretion capacity of *P. citrinopileatus* Han 1192 and *P. eryngii* Han 1205.

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