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ORIGINAL ARTICLE

Oxidative enzymes activity and hydrogen peroxide production in white-rot fungi and soil-borne micromycetes co-cultures

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Abstract

Fungal co-cultures appear to be advantageous for ligninolytic enzyme (LE) production compared to single fungal strains. The aims of this study were (1) to determine the type of fungal interactions in the co-cultures of two white-rot fungi (WRF, *Pycnoporus sanguineus* and *Trametes maxima*) and eight soil-borne micromycetes (SBM), (2) to determine the laccase and manganese peroxidase (MnP) activities and the hydrogen peroxide (H_2O_2) production in two compatible fungal and micromycetic co-cultures in submerged fermentation, and (3) to understand the effect of H_2O_2 on LE production by WRF through a dose-response bioassay. In the co-culture of SBM and *Pycnoporus sanguineus*, the main interaction was deadlock at a distance, whereas *T. maxima* showed competitive antagonism and replaced the SBM. In the agar plates, *Purpureocillium lilacinum* (27.8-fold increase) and *Beauveria brongniartii* (9.4-fold increase) enhanced the laccase and MnP activities of *P. sanguineus*, and *Metarhizium anisopliae* (Ma129) (0.83-fold increase) and *Trichoderma* sp. SP6 (22.6-fold increase) similarly enhanced these activities in *T. maxima*. In submerged fermentation, *P. lilacinum* also increased the laccase and MnP activities of *P. sanguineus*. The laccase activity of *T. maxima* only increased in the co-culture with *B. brongniartii*. The co-cultures achieved higher H_2O_2 production compared to the WRF monoculture, which played a vital role in the increase of LE. The dose-response assays revealed that low concentrations of H_2O_2 (2.94 and 14.69 mM) enhance the laccase and MnP activities in WRF.

Keywords Fungal co-culture · Hydrogen peroxide production · Laccase · Manganese peroxidase

Introduction

In the last decade, the number of studies on the mycoremediation of polluted water (Pan et al. 2014; Li et al. 2016) and soil (Yanto and Tachibana 2014; Yanto et al. 2017) using ligninolytic enzymes (LE) from fungal co-cultures, rather than single fungal strains, has significantly increased. According to Bader et al. (2010), a fungal co-culture is defined as an anaerobic or aerobic incubation of different fungal species under aseptic conditions. The utilization of fungal co-cultures appears to be advantageous over the use of a single fungal strain during numerous biotechnological processes, such as the production of LE (Pan et al. 2014), drug discovery (Bertrand et al. 2014a), metabolite production (Rateb et al. 2014), and lignin degradation (Song et al. 2011). Fungal co-cultures enable the synergistic utilization of the metabolic pathways of both species present in the co-culture (Bertrand et al. 2014b). In nature, most transformations (i.e., lignin and organic matter degradation) occur via the combined metabolic pathways of different microorganisms. In this context, the application of fungal co-cultures is one potential means of producing LEs for industrial (Kumar et al. 2018), environmental (Kumar et al. 2017), and biotechnological processes (Rateb et al. 2014; Baweja et al. 2016).

Fungal co-culture has been reported as an effective strategy for increasing the LE activities of white-rot fungi (WRF) under solid-state fermentation (Kuhar et al. 2015) and submerged fermentation (Díaz-Rodríguez et al. 2018). In particular, many studies have focused on the interactions between edible mushrooms (Basidiomycetes) and the micromycete genus *Trichoderma* (Deuteromycetes). Initially, these co-

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cultures were studied because *Trichoderma* was found to be an antagonistic fungus of edible mushrooms (Savoie and Mata 2003; Velázquez-Cedeño et al. 2004; Mata et al. 2005; Zhang et al. 2006; Flores et al. 2010). However, studies examining a wider range of WRF in co-cultures with soil-borne micromycetes (SBM) and their effects of LE production are scarce (Bader et al. 2010).

Additionally, the laccase (EC 1.10.3.2, p-diphenol oxygen oxidoreductase) and manganese peroxidase (MnP, *EC* 1.11.1.13) produced by WRF in co-culture systems have several environmental, industrial, and biotechnological applications (Kumar et al. 2017; Kumar et al. 2018; Zhong et al. 2018). For example, laccases are used to degrade endocrine disruptors (phytoestrogens, bisphenols, phthalates, antibiotics, organohalogenated compounds, and parabens) through mycoremediation (Barrios-Estrada et al. 2018) and are also widely used in the food (e.g., to remove phenols in wine), textile (e.g., to bleach denim fabrics), pulp and paper (e.g., to bleach pulp), and biofuel (e.g., to pretreat lignocellulose materials) industries as well as for organic synthesis of compounds (e.g., to synthesize anticancer drugs and antibiotics) (Rodríguez-Couto 2018). The biotechnological applications of laccases have recently been explored in the field of nanobiotechnology (i.e., the creation of a laccase-based biosensor; Das et al. 2017) and biomedicine (i.e., the detection of insulin, morphine, and codeine; Rodríguez-Couto 2018). Meanwhile, MnP has been successfully used for biopulping and bioleaching in the paper industry (Saleem et al. 2018), for azo dye decolorization in the textile industry (Sen et al. 2016; Zhang et al. 2018) and for the degradation of phenol compounds in bioethanol production (Rastogi and Shrivastava 2017). Both laccase and MnP from fungal co-cultures have been used simultaneously to degrade xenobiotics in the mycoremediation of petroleum hydrocarbons (Yanto and Tachibana 2014), indigo dye (Pan et al. 2014), atrazine (Chan-Cupul et al. 2016), malachite green (Kuhar et al. 2015), sulfamethoxazole (Li et al. 2016), and synthetic brilliant green industrial carpet dye (Kumari and Naraian 2016).

Despite recent advances, a wider range of fungal species needs to be studied to discover those that are capable of enhancing LE activities in WRF. The fungal interaction types between fungi in co-cultures also need to be determined. In addition, the role of specific molecules such as hydrogen peroxide on LE production needs to be further explored (Gönen 2018). Therefore, the objectives of this study were (1) to examine the types of interspecific interactions that occur between two WRF and eight SBM on agar plates in fungal co-cultures, (2) to determine the LE activities of WRF in co-cultures with SBM on agar plates, (3) to evaluate the LE activities and H_2O_2 production of two compatible fungal co-cultures (WRF-SBM) in submerged fermentation, and (4) to understand the effect of H_2O_2 on the LE production of WRF in submerged fermentation through a dose-response bioassay.

Materials and methods

Fungal source

Two WRF and eight SBM were used. One of the WRF, *Trametes maxima*, was isolated and identified by Chan-Cupul et al. (2016). The carpophore of another WRF, *Pycnoporus sanguineus*, was collected in Villa de Alvarez, Colima, Mexico (location 19°30′32.70″ N, 103°63′058″ W), and isolated using the methodology of Chaparro et al. (2009). The utilized SBM were obtained as follows: *Paecilomyces carneus* were donated, isolated, and identified by Heredia and Arias (2008). *Aspergillus* sp., *Beauveria brongniartii*, *Metarhizium anisopliae* (strains Ma129 and Ma258), *Penicillium hispanicum*, *Purpureocillium lilacinum*, and *Trichoderma* sp. (strain SP6) were isolated from agricultural soils in Colima, Mexico, and were reactivated in potato dextrose agar (PDA) from the Fungal Culture Collection of the Faculty of Biological and Agricultural Sciences of Colima University.

Co-cultures on agar plates

Fungal interspecific interactions were evaluated in dual culture experiments in Petri dishes (90 mm ø) containing 20 mL of modified Sivakumar (Sivakumar et al. 2010) culture medium containing the following (g/L): glucose (20), yeast extract (2.5), KH_2PO_4 (1.0), $(NH_4)_2SO_4$ (0.05), $MgSO_4$ (0.5), $CaCl_2$ (0.01), $FeSO_4$ (0.01), $MnSO_4$ (0.001), $ZnSO_4$ (0.001), $CuSO_4$ (0.002), and bacteriological agar (18). A 6-mm plug from the margin of a 7-day-old culture of WRF was inoculated on the border of a Petri dish to establish the co-culture; then, 5 μL of a SBM spore suspension (1×10^6 spores/mL) was inoculated on the other side of the Petri dish. Co-cultures were incubated in the dark at 75% relative humidity (RH) and 25 °C for at least 7 days. Petri dishes inoculated with individual fungal species were used as controls. For each co-culture, five replicates and their respective controls were used. A total of 18 co-cultures of the interactions between *T. maxima* or *P. sanguineus* and eight SBM were studied. The methods for evaluating the response variables are described below.

Antagonism index The antagonism of each species was determined using the rating scale proposed by Badalyan et al. (2002, 2004). The gross outcomes of combative interactions can be either replacement, where one fungus gains territory from the other, or deadlock, where neither fungus gains headway (Boddy, 2000). Three main types of interactions (A, B, or C) and four subtypes (C_{A1}, C_{B1}, C_{A2}, or C_{B2}) were identified. Type A and B are deadlock interactions consisting of mutual inhibition at mycelial contact (A) or at a distance (B) wherein neither organism is able to overgrow the other. Type C is fungal replacement and overgrowth without initial deadlock.

The intermediate subtypes are C_{A1} (partial), C_{A2} (complete replacement after initial deadlock at mycelial contact), C_{B1} (partial), and C_{B2} (complete replacement after initial deadlock at a distance). A score was assigned to each type or subtype of interaction: A = 1.0, B = 2.0, C = 3.0, C_{A1} = 3.5, C_{B1} = 4.0, C_{A2} = 4.5, and C_{B2} = 5.0. The antagonism index (AI) was then calculated for each species according to Badalyan et al. (2004) using Eq. 1, where n = number (frequency) of each type or subtype of interaction.

$$\begin{aligned} AI = {} & A(n \times 1.0) + B(n \times 2.0) + C(n \times 3.0) \\ & + C_{A1}(n \times 3.5) + C_{B1}(n \times 4.0) + C_{A2}(n \times 4.5) \\ & + C_{B2}(n \times 5.0) \end{aligned} \quad (1)$$

Determination of enzyme activities

The fungal enzyme extracts (FEE) were prepared by taking seven mycelial discs (6 mm Ø) from the deadlock zone of each co-culture and placing them in a test tube containing 7 mL of sterile distilled water. The test tubes were stirred for 2 h at 120 rpm in a horizontal shaker. Subsequently, the test tubes were centrifuged at 10,000×g for 10 min. Finally, the mycelium-free supernatant was collected from each sample to determine laccase and MnP activities.

Laccase The protocol from Sunil et al. (2011) was used to measure laccase activity using ABTS (2, 2′-azino-bis(3-ethylbenzthiazoline-6-sulfonic acid) (Sigma-Aldrich®, USA) as the substrate. The assay mixture contained 0.5 mM ABTS, 0.1 M sodium acetate buffer (pH 4.5), and a sufficient amount of FEE. ABTS oxidation was monitored at 420 nm (ε420, 3.6×10^4 M^{-1} cm^{-1}) during 5 min. One unit was defined as the amount of laccase that oxidized 1 μmol of ABTS substrate per minute. Laccase activity was expressed as volumetric activity (U/L).

Manganese peroxidase Manganese peroxidase activity was measured by the reduction of Mn^{3+} to Mn^{2+} in the presence of phenol red (Sigma-Aldrich®, USA) according to Glenn and Gold (1985). The oxidation of phenol red was measured at 610 nm (ε610, 22.0 mM^{-1} cm^{-1}). The reaction mixture contained 0.1 mM $MnSO_4$, 0.1 mM H_2O_2, 0.01% (wt./vol) phenol red, 25 mM lactate, 0.1% (wt./vol) bovine serum albumin, and 20 mM sodium succinate buffer (pH 4.5). The mixture was incubated for 5 min at room temperature. After incubation, the reaction was ended by the addition of NaOH (80 mM). One unit of MnP activity was the amount of enzyme needed to form 1 mmol of oxidized phenol red (mL/min). Manganese peroxidase activity in the FEE was expressed as volumetric activity (U/L).

Co-culture experiments in liquid fermentation

Two fungal co-cultures from the Petri dish bioassays were selected to study in liquid fermentation using Sivakumar culture medium without agar: *T. maxima-B. brongniartii* and *P. sanguineus-P. lilacinum*. Co-cultures were established in Erlenmeyer flasks (250 mL) with 120 mL of Sivakumar culture medium. Flasks were inoculated with three plugs of *T. maxima* or *P. sanguineus* (5 mm Ø) and three plugs of *B. brongniartii* or *P. lilacinum* (5 mm Ø); the SBM was added 3 days after inoculating the WRF. Monocultures of WRF and SBM were used as controls. Co-cultures and monocultures were incubated on a rotating shaker (120 rpm) at 25 °C and 75% RH for 4 days. Five replicates were established. Culture samples were collected daily. After being centrifuged (10,000×g, for 10 min), the supernatants were used to determine the H_2O_2 production and LE activities (laccase and MnP).

Hydrogen peroxide determination The content of H_2O_2 in the FEEs was determined using the iodide/iodate method according to Klassen et al. (1994). The blank absorbance was determined by substituting the FEE with a sterile Sivakumar culture medium in the reaction mixture. The content of H_2O_2 was then calculated by substituting with H_2O_2 reagent (30%, J. T. Baker™) according to absorbance along the standard curve at known concentrations ($y = 0.0303x + 0.0067$, $P < 0.05$, $r^2 = 0.992$).

Response of ligninolytic enzymes produced by white-rot fungi to H_2O_2 concentration

A dose-response assay was used to study the effect of H_2O_2 on laccase and MnP activities in WRF. Erlenmeyer flasks with Sivakumar culture medium (120 mL) were used for the monocultures of *T. maxima* and *P. sanguineus*; flasks were inoculated with three agar-mycelial plugs and incubated as mentioned previously. After 3 days, solutions of H_2O_2 were added to the flasks using a micropipette to obtain concentrations of 2.93, 14.69, 29.39, and 293.99 mM in the culture medium. Five replicates per sample were used to measure the H_2O_2 concentrations; a control without H_2O_2 was also included. Laccase and MnP activities were measured for 4 days.

Results and discussion

Antagonism index in interspecific interactions

Table 1 shows the AI for the fungal co-cultures of the WRF, *P. sanguineus* (Fig. 1) and *T. maxima* (Fig. 2), and the eight SBM. In the *P. sanguineus* co-cultures, inhibition at a distance (B) was the main type of interaction. The SBM that showed

Table 1 Antagonism index values and competitive reactions between the white-rot fungi: *Pycnoporus sanguineus* and *Trametes maxima* and soil-borne micromycetes in co-culture

Soil-borne micromycetes	White-rot fungi		AI
	P. sanguineus	*T. maxima*	
Beauveria brongniartii	B	A	3
Purpureocillium lilacinum	B	A	3
Penicillium hispanicum	B	C_{B1}	7
Trichoderma sp. (SP6)	C_{A1}*	C_{B2}*	7
Metarhizium anisopliae (Ma 129)	B	C_{A1}	5.5
Aspergillus sp.	A	C_{A1}	4.5
Paecilomyces carneus	B	B	4
Metarhizium anisopliae (Ma 258)	B	A	3

*Situation when the SBM was able to overgrowth and replaced the WRF

this interaction type were *B. brongniartii*, *P. lilacinum*, *P. hispanicum*, *M. anisopliae* (Ma 129 and Ma 258), and *P. carneus*. *Aspergillus* sp. achieved a deadlock with *P. sanguineus* (A). *Trichoderma* sp. (SP6) was able to overgrow and completely replace *P. sanguineus* (C_{A1}, Fig. 1).

Trametes maxima was competitive against *P. hispanicum* (C_{B1}), partially replacing this latter species after initial deadlock at a distance. In addition, *T. maxima* was slightly competitive against *Metarhizium anisopliae* (Ma 129) and *Aspergillus* sp. and was able to partially replace both micromycetes after exhibiting deadlock at mycelial contact (C_{A1}). On the other hand, *T. maxima* was completely replaced by *Trichoderma* sp. (SP6, C_{B2}). Additionally, some SBM such as *B. brongniartii*, *M. anisopliae* (Ma 258), and *P. lilacinum* appeared to be compatible with *T. maxima* and exhibited deadlock at mycelial contact (A). Finally, *P. carneus* showed deadlock at a distance against *T. maxima* (B, Fig. 2).

The evaluation of fungal interactions on agar plates is useful for selecting two compatible fungal strains and for subsequently testing their effect on the enhancement of ligninolytic enzyme activities in liquid cultures. Two fungal species that show deadlock at mycelial contact (interaction type A) are preferable in comparison to fungal interactions characterized by partial or complete replacement, as occurred with *Trichoderma* sp. and *T. maxima* (C_{B2}). In a previous study, Badalyan et al. (2004) reported that *Trichoderma* shows competitive antagonism against xylotrophic mushrooms, such as *Coriolus versicolor*, *Ganoderma lucidum*, *Polyporus varius*, and *Pleurotus ostreatus*, among others. In the present study, the main interactions were partial (C_{A1}) or complete (C_{A2}) replacement following deadlock.

Notably, *P. sanguineus* was unable to replace the SBM. Some strains of *P. ostreatus* can replace SBM such as *Trichoderma viride* and *Trichoderma pseudokoningii* (C_{A2} interaction type, Badalyan et al. 2004). In contrast, the studied strain of *Trichoderma* sp. SP6 was able to partially replace both *P. sanguineus* and *T. maxima*; these replacements led to an increase in laccase and MnP activities in both WRF. Dwivedi et al. (2011) reported inhibition at a distance between *Pycnoporus* sp. (MTCC 137) and *Penicillium oxalicum* (SAU_E-3.510) in agar plate interactions. Specifically, the mycelial growth of *Pycnoporus* sp. (MTCC 137) reduced while that of *P. oxalicum* increased. More recently, Arfi et al. (2013) reported on the ability of *Pycnoporus coccineus* to overgrow the mold *Botrytis cinerea* as well as the ability of *Coniophora puteana* to overgrow *P. sanguineus*. These fungal co-cultures led to an increase in the gene transcript level of 1343 (*B. cinerea*) to 4253 (*C. puteana*) in comparison to the monoculture of *P. coccineus*; transcripts converge toward a limited set of roles, including detoxification of secondary metabolites.

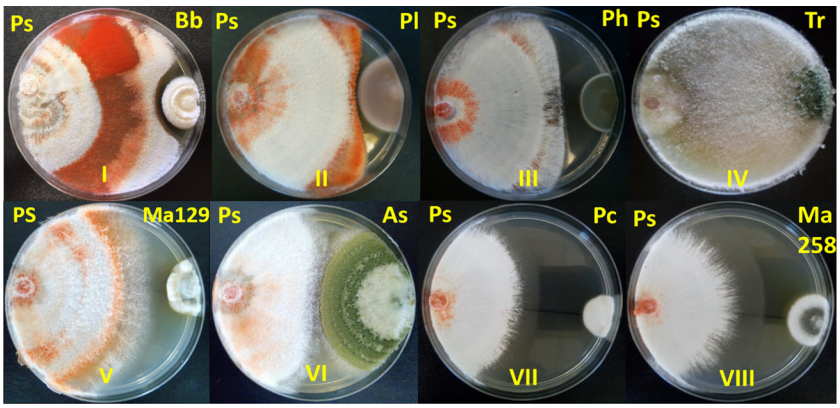

Fig. 1 Interspecific interactions types between *Pycnoporus sanguineus* (Ps) and soil-borne micromycetes: (I) deadlock at distance between *B. brongniartii* (Bb) and *P. sanguineus*, (II) deadlock at distance between *P. lilacinum* (Pl) and *P. sanguineus*, (III) deadlock at distance between *P. hispanicum* (Ph) and *P. sanguineus*, (IV) partial replacement of *P. sanguineus* after a deadlock at contact with *Trichoderma* sp. (SP6), (V) deadlock at distance between *M. anisopliae* (Ma 129) and *P. sanguineus*, (VI) deadlock at contact between *P. sanguineus* and *Aspergillus* sp. (As), (VII) deadlock at distance between *P. carneus* (Pc) and *P. sanguineus*, and (VIII) deadlock at distance between *M. anisopliae* (Ma 258) and *P. sanguineus*

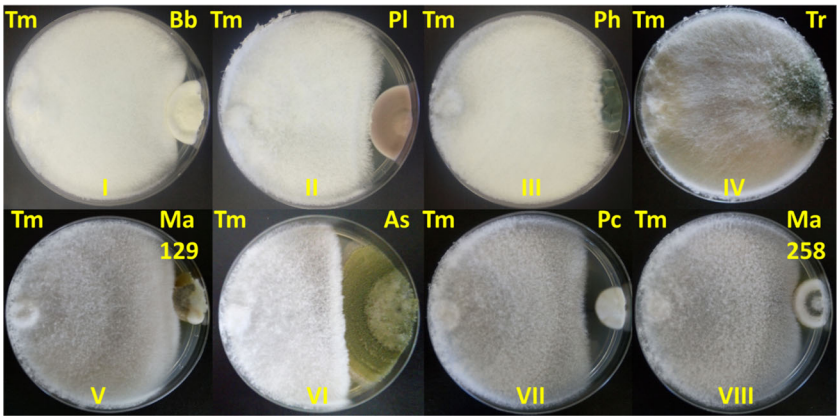

Fig. 2 Interspecific interactions between *T. maxima* (Tm) and soil-borne micromycetes: (I) inhibition at mycelial contact between *B. brongniartii* (Bb) and *T. maxima*, (II) inhibition at mycelial contact between *P. lilacinum* (Pl) and *T. maxima*, (III) partial replacement of *P. hispanicum* (Ph) by *T. maxima*, after an initial deadlock at distance, (IV) partial replacement of *T. maxima* by *Trichoderma* sp. (SP6), after an initial deadlock at mycelial contact, (V) partial replacement of *M. anisopliae* (Ma 129) by *T. maxima*, after an initial deadlock at mycelial contact, (VI) partial replacement of *Aspergillus* sp. (As) by *T. maxima*, after an initial deadlock at mycelial contact, (VII) inhibition at distance between *P. carneus* (Pc) and *T. maxima*, and (VIII) inhibition at mycelial contact between *M. anisopliae* (Ma 258) and *T. maxima*

In addition, barrages of brown pigments are commonly found in mycelial contact zones; these could be associated with ligninolytic enzyme activities, principally those of laccase, as well as with the formation of melanin compounds that protect fungal hyphae (*T. maxima*) from SBM attack. Also, mushrooms are known to release laccase as a defensive response against mycelial invasion. In this respect, enzymes help mushrooms to adapt to antagonistic environments or environmental stress (Divya and Sadasivan, 2016

Ligninolytic enzyme activities in agar plates

***Pycnoporus sanguineus* interactions** *Pycnoporus sanguineus* (1.6 U/L) significantly increased ($F = 8.41$, $P = 0.00001$) its laccase activity when co-cultured with *B. brongniartii* (27.6 U/L), *P. lilacinum* (47.2 U/L), *Trichoderma* sp. (30.1 U/L), *M. anisopliae* Ma129 (26.4 U/L), and *Aspergillus* sp. (14.1 U/L) on agar plates (Table 2). In particular, *P. lilacinum* achieved the highest fold increase in laccase activity (27.8) when co-cultured with *P. sanguineus*. Therefore, this fungal co-culture was selected for the submerged fermentation experiment. In regard to MnP activity, both *B. brongniartii* (9.4 U/L) and *P. lilacinum* (5.9 U/L) significantly enhanced ($F = 3.61$, $P = 0.0056$) the MnP activity of *P. sanguineus* (1.0 U/L) by 7.7- and 4.5-fold, respectively (Table 2).

The ligninolytic enzyme activity of *P. sanguineus* on agar plates under co-culture conditions has not been previously reported. However, Van Heerden et al. (2011) did demonstrate

Table 2 Laccase and MnP activities of *Pycnoporus sanguineus* in co-culture with soil-borne micromycetes in agar plates

Interactions	Laccase		MnP	
	Vol. activity (U/L)	Increase fold	Vol. activity (U/L)	Increase fold
P. sanguineus	1.6 ± 0.2 d	–	1.0 ± 0.5 c	–
P. sanguineus-B. brongniartii	27.6 ± 2.9 b	15.9 ± 1.78 b	9.4 ± 3.7 a	7.7 ± 3.1 a
P. sanguineus-P. lilacinum	47.2 ± 5.3 a	27.8 ± 3.24 a	5.9 ± 0.9 ab	4.5 ± 0.9 ab
P. sanguineus-P. hispanicum	2.8 ± 0.4 d	0.7 ± 0.24 d	2.8 ± 0.2 bc	1.6 ± 0.2 bc
P. sanguineus-Trichoderma sp.	30.1 ± 5.4 b	17.4 ± 3.28 b	1.5 ± 0.3 c	0.5 ± 0.1 c
P. sanguineus-M. anisopliae (Ma129)	26.4 ± 2.5 b	15.5 ± 1.52 b	3.1 ± 0.5 bc	1.8 ± 0.4 bc
P. sanguineus-Aspergillus sp.	14.1 ± 0.1 c	7.6 ± 0.57 c	1.9 ± 0.2 c	0.8 ± 0.2 c
P. sanguineus-P. carneus	3.7 ± 0.7 d	1.3 ± 0.41d	1.7 ± 0.4 c	0.6 ± 0.3 c
P. sanguineus-M. anisopliae (Ma258)	3.8 ± 0.2 d	1.3 ± 0.11 d	2.9 ± 0.7 bc	1.7 ± 0.7 bc
F =	8.41	12.65	4.02	3.61
P =	0.00001*	0.00001*	0.0017*	0.0056*

*Indicates significant values

Means with the same letter in row are not significantly different (LSD, $P = 0.05$). Vol, volumetric

Table 3 Laccase and MnP activities of *Trametes maxima* in co-culture with soil-borne micromycetes in agar plates

Interactions	Laccase		MnP	
	Vol. activity (U/L)	Increase fold	Vol. activity (U/L)	Increase fold
T. maxima (control)	67.5 ± 4.3 bc	–	1.1 ± 0.1 c	–
T. maxima-B. brongniartii	115.9 ± 13.2 a	0.72 ± 0.19 a	9.2 ± 1.5 b	6.8 ± 1.2 bc
T. maxima-P. lilacinus	69.9 ± 4.3 b	0.06 ± 0.01 b	11.1 ± 3.0 b	8.4 ± 2.5 b
T. maxima-P. hispanicum	30.4 ± 6.6 de	–	3.4 ± 0.9 c	1.9 ± 0.8 cd
T. maxima-Trichoderma sp. SP6	85.4 ± 13.3 b	0.55 ± 0.09 ab	28.0 ± 4.7 a	22.6 ± 3.9 a
T. maxima-M. anisopliae (Ma129)	123.7 ± 21.6 a	0.83 ± 0.31 a	2.7 ± 0.5 c	1.3 ± 0.4 d
T. maxima-Aspergillus sp.	61.3 ± 0.8 bc	–	1.5 ± 0.1 c	0.3 ± 0.1 d
T. maxima-P. carneus	10.1 ± 2.1 e	–	3.0 ± 0.5 c	1.5 ± 0.4 d
T. maxima-M. anisopliae (Ma258)	39.6 ± 5.3 cd	–	6.2 ± 1.3 bc	4.8 ± 1.2 bcd
F =	13.65	3.11	17.80	16.72
P =	0.00001*	0.0559*	0.00001*	0.00001*

*Indicates significant values

Means with the same letter in row are not significantly different (LSD, $P = 0.05$). Vol, volumetric

that co-cultures of *P. sanguineus* with *Aspergillus flavipes* in wood chips of *Acacia mearnsii*, *Eucalyptus dunnii*, *Eucalyptus grandis*, and *Eucalyptus macarthurii* altered the chemical composition of each tree species in different ways. Also, the authors demonstrated that the co-culture of *P. sanguineus-A. flavipes* resulted in a higher cellulose content and lower lignin content in degrading wood chips compared to the monoculture of *P. sanguineus* (Van Heerden et al. 2008). Given this context, fungal co-cultures could have relevant applications given the ecology of lignin decomposition, although ligninolytic enzymes were not evaluated by these previous authors.

***Trametes maxima* interactions** *Trametes maxima* (67.5 U/L) significantly increased ($F = 13.65$, $P = 0.00001$) its laccase activity when co-cultured with *B. brongniartii* (115.9 U/L) and *M. anisopliae* Ma129 (123.7 U/L) by 0.72- and 0.83-fold, respectively (Table 3). In addition, three species of SBM, *B. brongniartii* (9.2 U/L), *P. lilacinum* (11.1 U/L), and *Trichoderma* sp. SP6 (28.0 U/L) were able to significantly enhance ($P < 0.05$) the MnP activity of *T. maxima* (1.0 U/L). The highest fold increases in the MnP activity of *T. maxima* were 8.4 and 22.6, which were caused by *P. lilacinum* and *Trichoderma* sp. SP6, respectively (Table 3).

Studies of fungal co-cultures using *Trametes* sp. are scarce. In a previous study, Hiscox et al. (2010) co-cultured *Trametes versicolor* (216 mU/wet weight) with other basidiomycetes on agar plates. The results indicated that *Stereum gausapatum*, *Daldinia concentrica*, *Bjerkandera adusta*, and *Hypholoma fasciculare* enhanced the laccase activity of *T. versicolor* by 139- (3218.9 mU/wet weight), 3.06- (877.8 mU/wet weight), 3.03- (871.6 mU/wet weight), and 0.93-fold (417.1 mU/wet weight), respectively. These increases were higher than those produced by the SBM. The synthesis of enzymes by fungal organisms is known to differ between strains and species. For example, *T. versicolor* did not produce MnP activity in a study conducted by Hiscox et al. (2010). However, this enzyme was induced in co-cultures of *T. versicolor* and its fungal competitors; the highest production was found with *S. gausapatum*. Meanwhile, in the present study, the highest fold increase (22.6) was found with *Trichoderma* sp. SP6. More recently, Kuhar et al. (2015) studied the fungal co-culture of two basidiomycetes, *T. versicolor* and *Ganoderma lucidum*, on agar plates. Laccase activity in the fungal co-culture was 1.1 U/g, representing a 1.75-fold increase in comparison to the monocultures of *T. versicolor* (0.4 U/g) and *G. lucidum* (0.1 U/g).

Co-culture experiments in liquid fermentation

Co-culture of *Pycnoporus sanguineus* and *Purpureocillium lilacinum* *Purpureocillium lilacinum* significantly increased the laccase activity of *P. sanguineus* (48 h = 0.91 U/L and 96 h = 0.73 U/L) at 48 ($t = -4.7897$, $P = 0.0030$) and 96 h ($t = 2.1057$, $P = 0.0399$) of fermentation by 2.09- (2.81 U/L) and 2.64-fold (2.69 U/L), respectively (Fig. 3A). Meanwhile, MnP activity was strongly and significantly increased in the co-culture with *P. lilacinum* at 48 h. Specifically, in the co-culture, the laccase activity at 48 ($t = -8.4065$, $P = 0.0001$), 72 ($t = -28.4098$, $P = 1.25^{-07}$), and 96 h ($t = -50.7384$, $P = 3.93^{-09}$) was 24.19, 58.11, and 61.89 U/L, respectively; in the monoculture, the laccase activity was 9.49 (48 h), 5.90 (72 h), and 5.04 U/L (96 h, Fig. 3B). Thus, the laccase activity of the co-cultures increased by 1.55- (48 h), 8.83- (72 h), and 11.27-

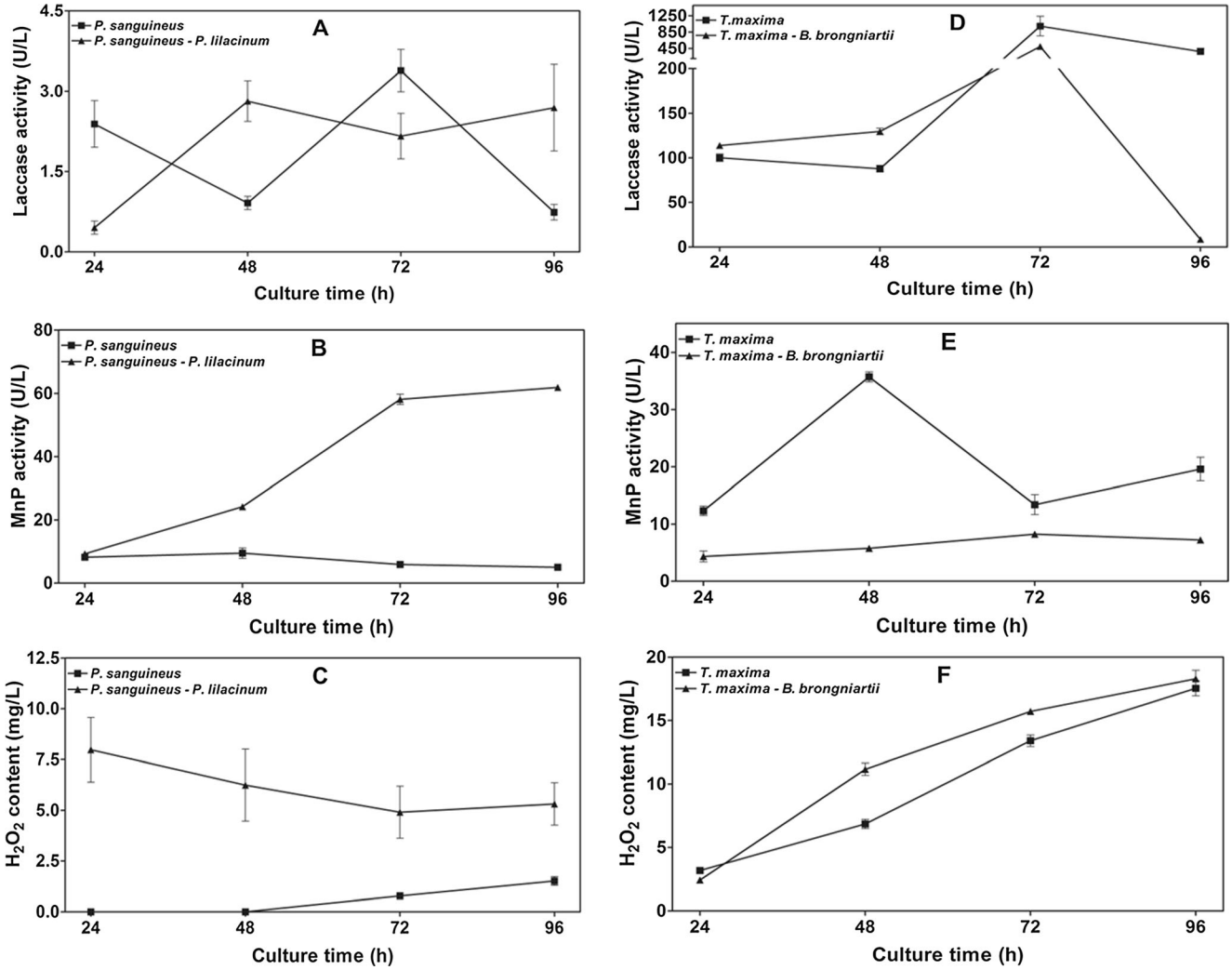

Fig. 3 Laccase (A and D) and MnP (B and E) activities, and H_2O_2 production (C and F) in two fungal co-cultures: *Pycnoporus sanguineus-Purpureocillium lilacinum* (A, B, and C) and *Trametes maxima-Beauveria brongniartii* (D, E, and F)

fold (96 h). The H_2O_2 content of the fungal co-culture extract was higher during the evaluation period compared to the monoculture extracts (Fig. 3C). Specifically, the H_2O_2 values in the co-culture ranged from 4.90 ($t = -3.2046$, $P = 0.0184$) to 7.97 mg/L ($t = -3.5567$, $P = 0.0119$), while those of the monocultures ranged from 0.78 to 1.50 mg/L.

However, in other studies, the laccase activities of *P. sanguineus* in monocultures were variable. Eugenio-Eugenio et al. (2009) and Vikineswary et al. (2006) reported values of 320 mU/L (0.32 U/L) in submerged fermentation and < 5.0 U/g of the substrate in solid-state fermentation, respectively. These values are low (Eugenio-Eugenio et al., 2009) and high (Vikineswary et al. 2006) with respect to those found for the co-culture of *P. sanguineus* and *P. lilacinum* (2.69 U/L), respectively. However, few data are available on *P. sanguineus* under co-culture conditions. Baldrian (2004) reported that *Trichoderma harzianum* was able to increase the laccase activity of *P. sanguineus* by 1.5-fold in liquid fermentation. Meanwhile, in the present study, laccase activity increased by 2.08- and 1.33-fold at 48 and 96 h of fermentation, respectively.

Co-culture of *Trametes maxima* and *Beauveria brongniartii*

The laccase activity of *T. maxima* increased in the presence of *Beauveria brongniartii* (24 h = 100.17 U/L and 48 = 87.77 U/L) at 24 ($t = -3.1653$, $P = 0.0194$) and 48 h ($t = -7.9183$, $P = 0.0002$) of fermentation. The laccase activities of the co-cultures were 113.87 and 129.66 U/L at 24 and 48 h, respectively, while the monoculture achieved 100.17 and 87.77 U/L in the same time frame (Fig. 4D). The MnP activity of *T. maxima* during the co-culture was not enhanced by *B. brongniartii* (Fig. 2E). The co-culture achieved the highest levels of H_2O_2 at 48 (11.16 mg/L, $t = -7.1149$, $P = 0.0003$) and 72 h (15.71 mg/L, $t = -4.7665$, $P = 0.0031$) in comparison to those of the *T. maxima* monoculture (48 h = 6.85 mg/L and 72 h = 13.40 mg/L).

Trametes (synonym of *Cerrena*) *maxima* was previously studied in co-culture with the basidiomycete *Coriolus*

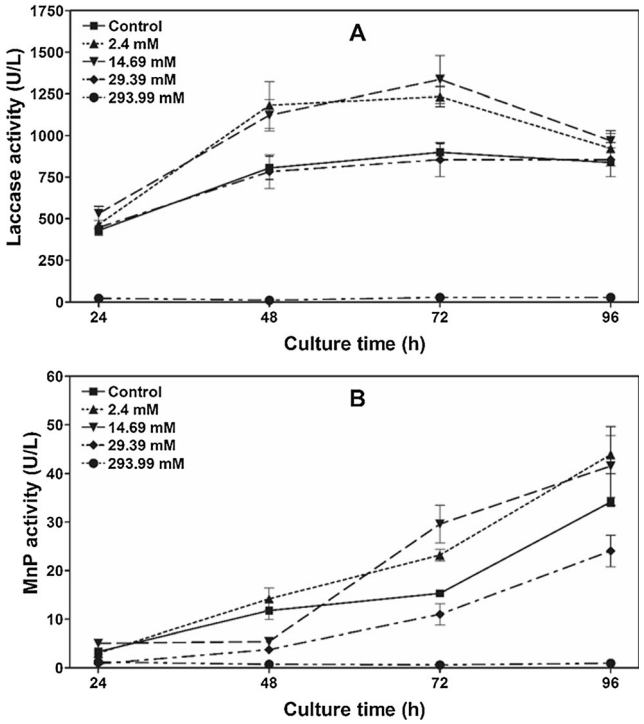

Fig. 4 Laccase (A) and MnP (B) activities of *Trametes maxima* under stress condition by hydrogen peroxide concentrations

hirsutus. In this case, both strains produced laccase at rates of approximately 63.0 and 415.0 nkatal/L respectively, in monocultures. However, these values were low compared to those of the co-culture of both species (510 nkatal/L, Koroleva et al. 2002). The levels of laccase achieved in the co-culture of these two strains represented a 7.1- and 0.22-fold increase compared to the monocultures of *Cucurbita maxima* and *C. hirsutus*, respectively. Baldrian (2004) reported that the SBM *T. harzianum*, *Acremonium sphaerospermum*, *Fusarium reticulatum*, *Humicola grisea*, and *Penicillium rigulosum* were able to increase the laccase activity of *T. versicolor* under liquid fermentation by 9-, 14-, 16.7-, 16-, and 55.6-fold, respectively, after 3 days of interaction.

Contrary to Koroleva et al. (2002), Baldrian (2004), and the present study, Xiao et al. (2004) reported that *Trametes* sp. AH28-2 reduced its laccase activity by 30% and 11% when co-cultured with *Aspergillus oryzae* and *Gloeophyllum trabeum*, respectively. More recently, Díaz-Rodríguez et al. (2018) reported that a non-laccase producing soil microfungi *Penicillium commune* GHAIE86 could increase the laccase activity of *Funalia floccosa* LPSC232 (20 mU/mL) by 3-fold (60 mU/mL) under submerged fermentation; in addition, *P. commune* was able to induce two laccase isoenzymes in *F. floccosa*. Interestingly, one function of SBM species appears to be the enhancement of laccase activity in WRF. However, the mechanisms behind and the reasons for this phenomenon are still under discussion.

Response of enzymes produced by white-rot fungi to H_2O_2 concentration

At 24 h of exposure to 14.69 mM (531.7 U/L) of H_2O_2, *T. maxima* (430.0 U/L) significantly ($F = 59.78$, $P = 0.00001$) enhanced its laccase activity by 0.23-fold. However, the highest concentration of H_2O_2 (293.99 mM) strongly inhibited laccase activity in *T. maxima* (Fig. 4A). At 48 ($F = 24.99$, $P = 0.00001$) and 72 h ($F = 35.35$, $P = 0.00001$) of exposure, both 2.93 and 14.69 mM of H_2O_2 led to significant increases in the laccase activity of *T. maxima*; the corresponding laccase values were 1182.0 and 1122.5 U/L, respectively, representing 0.46- (at 2.93 mM) and 0.39-fold (at 14.69 mM) increases, respectively. However, the highest H_2O_2 concentration caused strong inhibition of laccase activity at 48 and 72 h, corresponding with laccase activities of 11.3 and 28.1 U/L, respectively. At the end of the evaluation period, the laccase activity did not simply increase with increasing H_2O_2 concentration. The highest values of laccase activity ranged from 735.7 to 831.1 U/L, although the highest concentrations of H_2O_2 reduced the laccase activity to 32.6 U/L (Fig. 4A).

In regard to MnP activity (Fig. 4B), *T. maxima* significantly enhanced ($F = 110.31$, $P = 0.00001$) its MnP activity by 0.51-fold at 24 h of exposure to 14.69 mM of H_2O_2. Both 29.39 and 293.99 mM of H_2O_2 reduced the MnP activity of *T. maxima* from 3.35 U/L to 0.83 and 1.18 U/L, respectively (Fig. 2B). At 48 h, MnP activity was not increased by the H_2O_2 concentrations; instead, H_2O_2 concentrations of 14.69, 29.39, and 293.99 mM significantly inhibited MnP activity, leading to decreases of 11.75 U/L to 5.40, 3.75, and 0.73 U/L, respectively. At 72 and 96 h, the H_2O_2 concentrations of 2.93 and 14.69 mM were able to increase the MnP activities by 0.51- and 0.93-fold (at 72 h) and by 0.28- and 0.44-fold (96 h), respectively. As previously occurred, both 29.39 and 293.99 mM of H_2O_2 inhibited the MnP activity of *T. maxima* (Fig. 2B).

Pycnoporus sanguineus exhibited less laccase activity than *T. maxima*. However, *P. sanguineus* significantly increased its laccase activity under H_2O_2 stress. At 24 h of exposure, laccase activity in the *P. sanguineus* control was absent. However, the H_2O_2 concentrations of 14.69 mM and 29.39 mM activated laccase synthesis by *P. sanguineus*, leading to a laccase production of 4.15 and 5.94 U/L respectively (Fig. 5A). At 48 h, the H_2O_2 concentrations of 14.69, 29.39, and 293.99 mM enhanced the laccase activity of *P. sanguineus* (15.3 U/L) by 1.2- (34.9 U/L), 3.1- (63.1 U/L), and 1.5-fold (39.2 U/L). At 72 h, the H_2O_2 concentrations of 29.39 and 293.99 mM enhanced the laccase activity of *P. sanguineus* (17.32 U/L) by 68.8- (1210.5 U/L) and 36.3-fold (645.4 U/L). By the end of the experiment (96 h), 2.93 mM of H_2O_2 enhanced the laccase activity of *P. sanguineus* (56.12 U/L) by 14.71-fold (882.0 U/L, Fig. 5A).

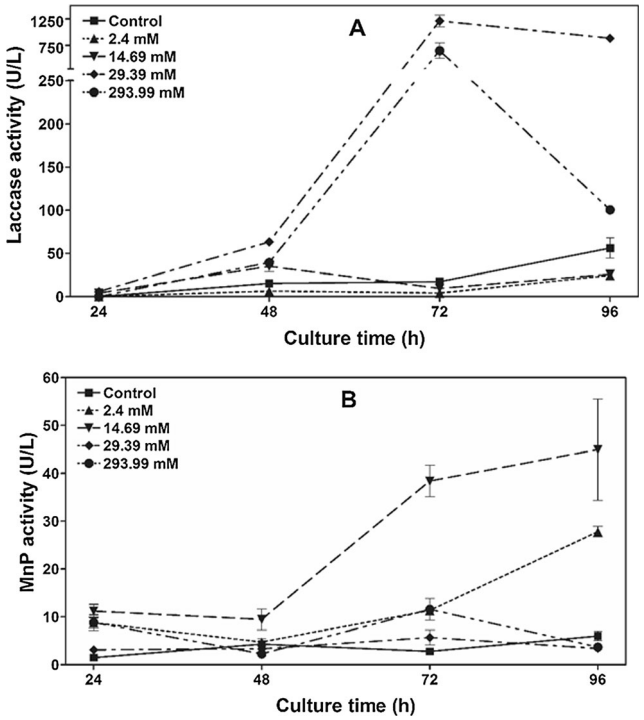

Fig. 5 Laccase (A) and MnP (B) activities of *Pycnoporus sanguineus* under stress condition by hydrogen peroxide concentrations

In regard to MnP activity (Fig. 5B), at 24 h, the H_2O_2 concentrations of 2.4 (8.7 U/L), 14.69 (11.1 U/L), and 293.99 (8.8 U/L) mM significantly ($F = 13.86$, $P = 0.0004$) enhanced the MnP activity of *P. sanguineus* (1.5 U/L) by 4.9-, 6.89-, and 5.0-fold, respectively. At 48 h, only 14.39 mM of H_2O_2 was required to significantly increase MnP activity ($F = 4.64$, $P = 0.0224$) by 1.8-fold. However, at 72 h, H_2O_2 concentrations of 2.93, 14.69, and 29.39 mM were required to achieve 3.0-, 12.8-, and 1.0-fold increases, respectively, in MnP activity, corresponding with MnP activities of 11.29, 38.40, and 5.68 U/L, respectively. Meanwhile, the control only achieved a MnP activity of 2.8 U/L. Finally, at the end of evaluation period (96 h), both 2.93 (27.8 U/L) and 14.69 (44.9 U/L) mM of H_2O_2 significantly increased ($F = 15.01$, $P = 0.0003$) the MnP activity of *P. sanguineus* (5.9 U/L), corresponding with 3.7- and 8.5-fold increases, respectively (Fig. 5B).

Hydrogen peroxide differentially increased the laccase activity of the WRF. This suggests that H_2O_2 could be responsible for the increase in laccase and MnP activities in fungal co-cultures, as the H_2O_2 in fungal extracts from both the *T. maxima-B. brongniartii* and the *P. sanguineus-P. lilacinum* co-cultures was high in comparison to the monocultures of both WRF. In fungal organisms, H_2O_2 plays an important role and influences enzymes activity. Branden et al. (1971) studied the interaction of a fungal laccase with H_2O_2 and found that H_2O_2 molecules are able to bind to one specific Cu^{2+} of the four copper atoms of the laccase molecule. This binding then modifies the absorbance of laccase and facilitates the removal of fluoride (a xenobiotic compound).

Furthermore, the catalytic activity of MnP is well known to be dependent on H_2O_2; however, this enzyme is also inactivated by excess H_2O_2. According to Bermek et al. (2002), the oxidation of native MnP by an equivalent amount of H_2O_2 forms active compound I, which subsequently oxidizes Mn^{2+} to Mn^{3+}. In this process, compound II is formed and reduced back to the native MnP, oxidizing an additional Mn^{2+} to Mn^{3+}. Mn^{2+} is a mandatory substrate for compound II. When excess concentrations of H_2O_2 are present, native MnP is directly converted to compound III, which is an inactive form of the enzyme. In addition, Li et al. (1995) demonstrated that the white-rot fungus *Phanerochaete chrysosporium* produces MnP mRNA following the addition of a low amount of H_2O_2 in the absence of Mn^{2+}, the natural substrate of MnP. These responses were observed in this study, as low amounts of H_2O_2 (2.93 and 14.69 mM) stimulated MnP activity, whereas high amounts (29.39 and 293.99 mM) inhibited MnP activity.

The source of H_2O_2 in co-culture systems is unclear and will be the target of future studies. However, both WRF and SBM are able to produce different levels of H_2O_2 via distinct metabolic pathways. Similarly, Urzúa et al. (1998) reported that *Ceriporiopsis subvermispora* is able to generate H_2O_2 through the oxidation of the organic acids that it secretes. Also, SBM are known to produce H_2O_2 as a result of glucose degradation by glucose oxidase (GOx), especially under the stress conditions caused by xenobiotics, as reported by Zúñiga-Silva et al. (2016).

Conclusions

In this study, the interspecific interactions and enzyme activities of the co-cultures of two WRF and eight SBM were evaluated in addition to the effects of H_2O_2 on WRF. The main type of interspecific interaction exhibited by the WRF *Pycnoporus sanguineus* was deadlock at a distance, while *T. maxima* partially replaced three of the studied SBM, confirming its dominance. *Purpureocillium lilacinum* enhanced to a large extent the laccase activity of *P. sanguineus*, and *B. brongniartii* was the principal enhancer of the MnP activity of *P. sanguineus*. Both *B. brongniartii* and *M. anisopliae* (Ma129) were the best enhancers of laccase activity in *T. maxima*, while *Trichoderma* sp. (SP6) increased the MnP activity of *T. maxima* to a large extent. In submerged fermentation, *P. sanguineus* increased its laccase and MnP activity in co-culture with *P. lilacinum*. Meanwhile, *T. maxima* did not increase its MnP activity but did slightly increase its laccase activity at the initial evaluation points. Finally, the co-cultures *P. sanguineus-P. lilacinum* and *T. maxima-B. brongniartii* achieved higher H_2O_2 production in comparison

to the WRF monocultures, suggesting that H_2O_2 plays an essential role in increasing ligninolytic enzyme activities. This conclusion was also confirmed by the dose-response assays, wherein low concentrations of H_2O_2 (2.94 and 14.69 mM) enhanced the laccase and MnP activities of *P. sanguineus* and *T. maxima*.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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