Fundación Miguel Lillo
Tucumán
Argentina

Lignin degradation by co-cultured fungi: current status and future perspectives

Degradação da lignina por fungos co-cultivados: estado atual e perspectivas futuras

Soares, Jullio K. Castro[1*]; Vera M. Valle Vitali[2]; Marcelo A. Vallim[1]

[1] Universidade Federal de São Paulo (UNIFESP), campus Diadema, R. São Nicolau, 210, Centro, Diadema, São Paulo, Brazil.
[2] Instituto de Pesquisas Ambientais (IPA), Av. Miguel Stéfano, 3687, São Paulo, Brazil.
* Corresponding author: <jullio.kennedy@unifesp.br>

ABSTRACT

The lignocellulosic biomass is a highly abundant and renewable resource. However, its exploitation is limited by the recalcitrance of the lignin present in the plant cell wall. In the last three decades, fungal co-cultures have increasingly been applied to overcome lignin recalcitrance by enhancing the production of ligninolytic enzymes through microbial interactions. In this paper, we systematically compile studies on fungal co-cultures used in the degradation of lignin-containing substrates to clarify the advantages and limitations of this type of culture. Based on their different delignification rate potentials, co-cultures can be classified into synergistic, antagonistic, and neutral. Co-cultivation results are generally related to the balance or imbalance of antagonistic and synergistic effects arising from the specific compatibility between the species during the interaction. It is well known that the paired species and the microenvironmental system conditions are responsible for the reported degradations, however, the mechanisms underlying these interactions remain poorly understood. In conclusion, literature results demonstrate the promising application of fungal co-cultures in biotechnological sectors to improve the degradation of lignin and its derivatives, through their better understanding of the efficient exploitation of biological resources on ecological and industrial scales.

Keywords — Co-culture; Delignification; Fungi; Lignocellulose; Review.

➤ Ref. bibliográfica: Soares, J. K. C.; Vitali, V. M. V.; Vallim, M. A. 2022. Lignin degradation by co-cultured fungi: current status and future perspectives. *Lilloa 59* (Suplemento): 39-62. **doi**: https://doi.org/10.30550/j.lil/2022.59.S/2022.08.10
➤ Recibido: 29 de junio 2022 – Aceptado: 10 de agosto 2022 – Publicado en línea: 18 de octubre 2022.
➤ URL de la revista: http://lilloa.lillo.org.ar

RESUMO

A biomassa lignocelulósica corresponde a uma fonte de recurso altamente abundante e renovável, porém, sua exploração é limitada pela recalcitrância fornecida pela lignina presente na parede celular vegetal. Uma abordagem crescente nas últimas três décadas se destina a aplicação de co-culturas fúngicas com o objetivo de aumentar a produção de enzimas ligninolíticas pelas interações microbianas, de forma a superar a recalcitrância da lignina. Neste artigo, compila-se sistematicamente os estudos de co-culturas fúngicas usadas na degradação de substratos com lignina de forma a esclarecer as vantagens e limitações deste tipo de cultivo. Quando comparado às respectivas culturas axênicas, as co-culturas podem ser classificadas em sinérgicas, antagônicas e neutras para agrupar os seus diferentes potenciais de taxa de deslignificação. Em geral, os resultados dos co-cultivos demonstram estarem relacionados com o equilíbrio ou desbalanço dos efeitos antagônicos e sinérgicos decorrentes da compatibilidade específica entre as espécies envolvidas durante a interação. Por mais que se tenha conhecimento que as espécies pareadas, em conjunto com as condições microambientais do sistema, sejam responsáveis pelas degradações relatadas, os mecanismos subjacentes às interações ainda permanecem incompreendidos. Em conclusão, os achados compilados da literatura demonstram a aplicação promissora de co-culturas fúngicas em setores biotecnológicos que visam intensificar a degradação de lignina e seus derivados, mediante a sua melhor compreensão em escala ecológica e industrial para a exploração eficiente de seu potencial biológico.

Palavras-chaves — Co-cultura; Deslignificação; Fungos; Lignocelulose; Revisão.

INTRODUCTION

Lignocellulosic biomass is a natural, renewable, and self-sustaining material promising for biotechnological applications. However, the targeted extraction of carbohydrate components (cellulose and hemicellulose) from the plant cell wall is restricted by the lignin polymer present as the third main constituent of this biomass type (Guerriero *et al.*, 2016). Lignin is formed by radical polymerization of three monomers (p-phenyl, guaiacyl, and syringyl) resulting in non-ordered and non-hydrolyzable bonds responsible for its complexity (Vanholme *et al.*, 2010; Chen, 2014). Lignin is not only difficult to degrade but also associates with carbohydrates to form a lignocellulosic matrix that restricts the access of hydrolytic enzymes and is resistant to physical, chemical, and biological degradation (Abdel-Hamid *et al.*, 2013).

Terrestrial fungi are among the microorganisms capable of overcoming lignin recalcitrance, allowing the degradation of lignocellulosic materials for better biotechnological exploitation. They stand out for their diverse enzymes and enzyme complexes capable of oxidizing the lignin polymer into smaller and assimilative structures (Dashtban *et al.*, 2010; Lundell *et al.*, 2014). A growing approach to stimulate ligninolytic enzyme production is through co-culture, characterized by two or more microorganisms incubated in a system under aseptic conditions instead of a single microbial species in axenic culture (Bader *et al.*, 2010).

This procedure based on co-culturing simulates the natural fungal community with various metabolic pathways, a greater number of enzymes, and even new enzyme isotypes based on the interaction of adjacent mycelia. Proximity stimulates the expression of groups of silenced genes, however, the molecular mechanisms of this induction remain partially unknown (Yao *et al.*, 2016). Transcriptome (Arfi *et al.*, 2013, Zhong *et al.*, 2019), proteome (Adav *et al.*, 2012), metabolome (Bertrand *et al.*, 2013a) and enzyme profiling (White and Boddy, 1992; Score *et al.*, 1997; Iakovlev and Stenlid, 2000; Tsujiyama and Minami, 2005) studies emphasize the ability of co-cultures to amplify system chemodiversity compared to corresponding axenic cultures, including compounds (Bertrand *et al.*, 2013b) and the enzymes (Zhang *et al.*, 2019) still unknown in the databases.

Despite the benefits of co-culturing and their potential to influence lignin degradation rates, fungal applications for converting lignocellulosic substrates are still predominantly performed using axenic cultures due to the greater control that this type of incubation provides. In this review, we provide an overview of the ligninolytic potential of fungal co-cultures by systematically searching the online literature for documented studies supporting their application for biotechnological purposes.

MATERIAL AND METHODS

The systematic search for scientific articles was carried out using the following eleven databases and search engines as research platforms: American Society for Microbiology; Biotechnology and BioEngineering; Google Scholar; Microbiology Society; Portal de Periódicos da CAPES; PubMed; SciELO; ScienceDirect; Scopus; Springer Link and Web of Science.

The surveyed records were screened using the Rayyan online platform, based on the inclusion criteria: (1) experimental studies in scientific articles format; (2) published virtually from January 1, 1990, to July 21, 2021; (3) written in English, Spanish or Portuguese; (4) measured lignin degradation by fungal co-cultures and at least one of their axenic cultures. In addition, all eligible articles were subjected to the Snowballing technique through the SnowGlobe online platform to improve the retrieval of relevant articles (Horsley *et al.*, 2011).

The selected scientific articles had their final relevance determined by reading the complete record concomitantly with data extraction, seeking information on the quantitative or qualitative abilities of fungal co-cultures to degrade lignin compared to their respective axenic cultures, besides identifying the factors that hypothetically or experimentally explain the observed effects and the scientific gaps.

RESULTS AND DISCUSSION

The estimate of the amount of available lignin in the biosphere is approximately 300 billion tons, with an annual increase of about 20 billion tons. When using lignocellulosic biomass, part of this amount accumulates as a by-product of different industries without proper disposal (Becker and Wittmann, 2019). However, the non-uniform

structure, the low chemical reactivity, and impurities limit the application of lignin, which is generally burned to generate energy. Therefore, lignin depolymerization is considered one of the critical challenges for its utilization (Chio *et al.*, 2019).

Fungi are the most studied microorganisms for lignin degradation due to their adaptation to colonize the resources containing this component. However, since these organisms extend their mycelia throughout the substrate, eventual proximity or contact with other mycelia competing for territory is inevitable. Therefore, ecological interactions contribute significantly to fungal communities' dynamic and structure. Thus, it is possible to take advantage of these interactions to simulate the natural environment of these microorganisms, positively interfering with the biodelignification of the colonized substrate (Boddy *et al.*, 1989; Owens *et al.*, 1994).

Research on interactions between fungi in dual co-cultures has been conducted to understand the complexity of mechanisms involved during the interactions (Dullah *et al.*, 2021). These interactions were also observed between fungi growing on decaying wood, indicating that they not only occur in the laboratory (Rayner and Boddy, 1988; Boddy, 2000). However, these results should be taken cautiously, once laboratory simulations may not always reflect the natural environment (Holmer and Stenlid, 1993).

The co-culture has received increasing research attention due to its favorable strain compatibility characteristics. In this context, compatibility refers to favorable interactions with increased enzymatic activity (Sperandio and Filho, 2019). However, its main disadvantage is the lack of information on its operational dynamics. The 43 studies available on lignin degradation by fungal co-cultures and their respective axenic cultures under sterile conditions are summarized in Table 1.

The highest lignin degradation observed was 68.0% by *Coriolus hirsutus* and *Cerrena maxima* co-cultures on sulfonated lignin substrate (Koroleva *et al.*, 2002) and 56.5% by *Phanerochaete chrysosporium* and *Trichoderma viride* co-culture on oat straw (Zhou and Li, 2016).

On the other hand, some authors identified that both co-cultures and axenic cultures were unable to degrade lignin with rates of 0%. This result can be due to the absence of ligninolytic potential (Karpe *et al.*, 2014; Cui *et al.*, 2015), the intensive holocellulose hydrolysis by the fungi (Carvalheiro *et al.*, 1994; Ezeonu *et al.*, 2016) or the sterilization with temperature and pressure variation (van Heerden *et al.*, 2008), which caused a concomitant increase in the relative lignin content.

Based on the co-culture rate of lignin degradation compared to their respective axenic cultures and the available statistical analyses, co-cultures can be classified into three main groups (synergistic, antagonistic, or neutral) according to the effects of interactions on their ligninolytic potential.

Table 1 (page 1 of 3). Summary of literature results on the rate of lignin degradation by fungal co-cultures and their respective axenic cultures. The final results of the co-cultures can be Synergistic (S), Neutral (N) or Antagonistic (A).

Tabela 1 (folha 1 de 3). Resumo dos resultados da literatura sobre a taxa de degradação da lignina por co-culturas fúngicas e suas respectivas culturas axênicas. Os resultados finais das co-culturas podem ser sinérgicos (S), neutros (N) ou antagônicos (A).

Reference	Substrate	Incubation time (days)	Species* (Abbreviation)	% of lignin degradation		Final result of co-cultivation
				Axenic cultures	Co-cultures	
Albert and Pandya (2013)	Bamboo thatch	30	*Daedaleopsis confragosa (Dc)* *Irpex lacteus (Il)* *Pycnoporus sanguineus (Ps)*	19 (Dc) 20 (Il) 23 (Ps)	23 (Dc-Ps) 26 (Dc-Il)	**2 S**
Arora (1995)	Wheat straw	30	*Chaetomium globosum (Cg)* *Daedalea flavida (Df)* *Fusarium moniliforme (Fm)* *Phanerochaete chrysosporium (Pc)* *Polyporus palustris (Ppa)* *Postia placenta (Ppl)* *Pycnoporus sanguineus (Ps)*	7 (Cg) 17 (Df) 6 (Fm) 29 (Pc) 6 (Ppa) 0 (Ppl) 17 (Ps)	29 (Df-Ps) 36 (Df-Pc) 32 (Pc-Ps) 19 (Df-Ppl) 14 (Df-Ppa) 19 (Ps-Ppl) 18 (Ps-Ppa) 29 (Pc-Ppl) 29 (Pc-Ppa) 13 (Df-Fm) 21 (Df-Cg) 13 (Ps-Fm) 14 (Ps-Cg) 18 (Pc-Fm) 33 (Pc-Cg)	**1 S** (Df-Ps) **20 N** (Df-Pc, Pc-Ps, Df-Ppl, Df-Ppa, Ps-Ppl, Ps-Ppa, Pc-Ppl, Pc-Ppa, Df-Fm, Df-Cg, Ps-Fm, Ps-Cg, Pc-Fm, Pc-Cg, Cg-Fm, Cg-Ppa, Cg-Ppl, Fm-Ppa, Fm-Ppl, Ppa-Ppl)
Asiegbu *et al*. (1996)	Spruce wood	42	*Phanerochaete chrysosporium (Pc)* *Pleurotus sajor-caju (Ps)* *Trametes versicolor (Tv)*	6 (Pc) 0 (Ps) 5 (Tv)	8 (Pc-Ps) 14 (Pc-Tv) 14 (Ps-Tv) 16 (Pc-Ps-Tv)	**4 S**
Bergbauer *et al*. (1992)	Reed stems	25	*Candelabrum spinulosum (Cs)* *Helicodendron luteoalbum (Hl)* *Helicomyces roseus (Hr)* *Helicosporium phragmitis (Hp)* *Spirosphaera floriformis (Sf)*	2 (Cs) 3 (Hl) 3 (Hr) 3 (Hp) 4 (Sf)	2 (Cs-Hl-Hr-Hp-Sf)	**1 A**
Carabajal *et al*. (2012)	Wheat straw	120	*Pleurotus citrinopileatus (Pc)* *Pleurotus ostreatus (Po)*	11 (Pc) 29 (Po)	23 (Pc/Po) 6 (Po/Pc) 17 (Pc+Po)	**3 N**
Carvalheiro *et al*. (1994)	Tomato bagasse	20	*Sporotrichum sp. (Ssp)* *Trichoderma reesei (Tr)*	0 (Ssp) 0 (Tr)	0 (Ssp-Tr)	**1 N**
Chen *et al*. (2015)	Rice straw	30	*Aspergillus niger (An)* *Trichoderma viride (Tv)*	NA (An) NA (Tv)	NA (An-Tv)	**1 S**
Chi *et al*. (2007)	Poplar wood	42	*Ceriporiopsis subvermispora (Cs)* *Phanerochaete chrysosporium (Pc)* *Pleurotus ostreatus (Po)* *Physisporinus rivulosus (Pr)*	54 (Cs) 25 (Pc) 16 (Po) 50 (Pr)	52 (Pr-Po) 54 (Cs-Po) 15 (Pc-Po) 54 (Pr-Cs) 35 (Pr-Pc)	**5 N**
Cui *et al*. (2015)	Vinegar residue	7	*Aspergillus ficuum (Af)* *Aspergillus niger (An)* *Phanerochaete chrysosporium (Pc)* *Trichoderma koningii (Tk)*	0 (Af) 0 (An) 0 (Pc) 0 (Tk)	4 (Af-An-Pc-Tk)	**1 S**
Cui *et al*. (2021)	Pure lignin	17	*Lenzites betulinus (Lb)* *Trametes versicolor (Tv)*	27 (Lb) 37 (Tv)	50 (Lb-Tv)	**1 S**

Table 1 (page 2 of 3).
Tabela 1 (folha 2 de 3).

Reference	Substrate	Incubation time (days)	Species* (Abbreviation)	% of lignin degradation		Final result of co-cultivation
				Axenic cultures	Co-cultures	
Darwish *et al*. (2012)	Corn stems	28	*Pleurotus ostreatus (Po)* *Saccharomyces cerevisiae (Sc)*	30 (Po)	46) (Po-Sc 15 mL) 47) (Po-Sc 30 mL) 49) (Po-Sc 45 mL)	**3 S**
Ezeonu *et al*. (2016)	Rice husk	7	*Trichophyton mentagrophytes (Tm)* *Trichophyton soudanense (Ts)*	0 (Tm) 0 (Ts)	0 (Tm-Ts)	**1 N**
Fatma *et al*. (2021)	Wheat straw	35	*Monascus purpureus (Mp)* *Trichoderma reesei (Tr)*	41 (Mp) 38 (Tr)	45 (Mp-Tr)	**1 S**
Feng *et al*. (2015)	Wheat straw	10	*Candida tropicalis (Ct)* *Pycnoporus sanguineus (Ps)*	20 (Ps)	23 (Ct-Ps)	**1 S**
Feng *et al*. (2016)	Wheat straw	10	*Candida tropicalis (Ct)* *Pycnoporus sanguineus (Ps)*	39 (Ps)	45 (Ct-Ps)	**1 S**
Gamal *et al*. (2014)	Sugarcane bagasse	28	*Ceriporiopsis subvermispora (Cs)* *Ophiostoma piliferum (Op)*	11 (Op)	45 (Cs-Op)	**1 S**
Giles *et al*. (2014)	Pine wood	30	*Ceriporiopsis subvermispora (Cs)* *Pleurotus ostreatus (Po)*	0 (Cs) 7 (Po)	6 (Cs-Po)	**1 N**
Giles *et al*. (2015)	Tulip wood	30	*Ceriporiopsis subvermispora (Cs)* *Postia placenta (Pp)*	0 (Cs) 0 (Pp)	7 (Cs-Pp)	**1 N**
Hermosilla *et al*. (2018)	Wheat straw	20	*Ganoderma lobatum (Gl)* *Gloeophyllum trabeum (Gt)*	31 (Gl) 0 (Gt)	25 (Gl-Gt)	**1 N**
Jamal *et al*. (2015)	Fruit peels	7	*Lentinus tigrinus M6 (M6)* *Lentinus tigrinus RO2 (RO2)* *Phanerochaete chrysosporium (Pc)*	NA (M6-RO2)	NA (M6-Pc) NA (RO2-Pc)	**2 S**
Karpe *et al*. (2014)	Grape waste	7	*Aspergillus niger (An)* *Penicillium chrysogenum (Pch)* *Penicillium citrinum (Pci)* *Trichoderma harzianum (Th)*	0 (An) 5 (Pch) 0 (Pci) 0 (Th)	18 (An-Pch-Pci-Th)	**1 S**
Kaur *et al*. (2018)	Rice straw	10	*Phanerochaete chrysosporium (Pc)* *Pleurotus ostreatus (Po)* Isolado ligninolítico *(LS1)*	20 (Pc) 21 (Po) 18 (LS1)	23 (Po-LS1) 11 (Pc-LS1) 30 (Pc-Po)	**2 S** (Po-LS1, Pc-Po) **1 A** (Pc-LS1)
Ke *et al*. (2011)	Rapeseed straw	50	*Candida utilis (Cu)* *Ganoderma lucidum (Gl)*	36 (Gl)	53 (Gl-Cu)	**1 S**
Koroleva *et al*. (2002)	Sulfonated lignin	45	*Coriolus hirsutus (Ch)* *Cerrena maxima (Cm)*	58 (Ch) 45 (Cm)	68 (Ch-Cm)	**1 S**
Kuhar *et al*. (2015)	Poplar wood	14	*Ganoderma lucidum (Gl)* *Trametes versicolor (Tv)*	38 (Gl) 61 (Tv)	40 (Gl-Tv)	**1 N**
Li *et al*. (2021)	Rice straw	56	*Gloeophyllum trabeum (Gt)* *Phanerochaete chrysosporium (Pc)*	0 (Gt) 27 (Pc)	0 (Gt-Pc)	**1 N**
Luo *et al*. (2020)	Alkaline lignin	21	*Irpex lacteus (Il)* *Phanerochaete chrysosporium (Pc)*	23 (Il) 22 (Pc)	30 (Il-Pc)	**1 S**
Ma *et al*. (2011)	Corn straw	25	*Auricularia polytricha (Ap)* *Irpex lacteus (Il)*	36 (Ap) 45 (Il)	45 (Ap-Il)	**1 N**

Table 1 (page 3 of 3).
Tabela 1 (folha 3 de 3).

Reference	Substrate	Incubation time (days)	Species* (Abbreviation)	% of lignin degradation		Final result of co-cultivation
				Axenic cultures	Co-cultures	
Meehnian *et al*. (2017)	Cotton stems	40	*Daedalea flavida (Df)* *Phlebia radiata (Pr)*	20 (Df) 15 (Pr)	23 (Df-Pr)	**1 S**
Nazarpour *et al*. (2013)	Rubber tree wood	90	*Ceriporiopsis subvermispora (Cs)* *Trametes versicolor (Tv)*	45 (Cs) 34 (Tv)	38 (Cs-Tv)	**1 N**
Qadir *et al*. (2018)	Sugarcane bagasse	3	*Candida tropicalis (Ct)* *Saccharomyces cerevisiae (Sc)*	28 (Ct) 19 (Sc)	9 (Ct-Sc)	**1 A**
Sasongko *et al*. (2019)	Rice straw	21	*Phanerochaete chrysosporium (Pc)* *Trichoderma viride (Tv)*	22 (Pc) 4 (Tv)	10 (Pc-Tv)	**1 N**
	Birch wood[1]			22[1] (Gt) 25[1] (Il)	26[1] (Gt-Il)	
Song *et al*. (2012)	Oak wood[2]	56	*Gloeophyllum trabeum (Gt)* *Irpex lacteus (Il)*	1[2] (Gt) 21[2] (Il)	27[2] (Gt-Il)	**3 N**
	Pine wood[3]			28[3] (Gt) 31[3] (Il)	26[3] (Gt-Il)	
Stepanova *et al*. (2003)	Oat straw	60[4] and 120[5]	Isolado ligninolítico *(IL)* *Trichoderma reesei (Tr)*	25□ (IL)	32□ (IL-Tr)	**1 S**
Tao *et al*. (2016)	Corn stem	10	*Aspergillus niger (An)* *Phanerochaete chrysosporium (Pc)* *Trichoderma viride (Tv)*	6 (Pc)	10 (Pc-An) 12 (Pc-Tv)	**2 S**
van Heerden *et al*. (2008)	Eucalyptus wood	14	*Aspergillus flavipes (Af)* *Pichia guilliermondii (Pg)* *Pycnoporus sanguineus (Ps)* *Rhodotorula glutinis (Rg)*	0 (Ps)	0 (Ps-Pg) 0 (Ps-Af) 0 (Ps-Pg-Rg)	**3 N**
Vasil'chenko *et al*. (2004)	Oat straw	36	Isolado ligninolítico *(IL)* Isolado celulolítico *(IC)*	30 (IL) 15 (IC)	15 (IL-IC)	**1 N**
Wang *et al*. (2014)	Poplar wood	84	*Lenzites betulinus (Lb)* *Trametes orientalis (To)* *Trametes velutina (Tv)*	45 (Lb) 47 (To) 58 (Tv)	45 (Lb-To) 46 (Lb-Tv) 42 (To-Tv)	**2 N** (Lb-To, Lb-Tv) **1 A** (To-Tv)
Xie *et al*. (2020)	Poplar bark	21	*Ceriporiopsis subvermispora (Cs)* *Coprinus cinereus (Cc)* *Pleurotus ostreatus (Po)*	41 (Cs) 27 (Cc) 23 (Po)	40 (Cs-Cc) 34 (Cs-Po) 29 (Cc-Po) 48 (Cs-Cc-Po)	**4 S**
Yang *et al*. (2011)	Alkaline lignin	12	*Aspergillus sp. (Asp)* *Pleurotus ostreatus (Po)*	23 (Asp) 65 (Po)	53 (Asp-Po)	**1 N**
Yang *et al*. (2013)	Pumpkin waste	7	*Phanerochaete chrysosporium (Pc)* *Trichoderma reesei (Tr)*	28 (Pc) 10 (Tr)	44 (Pc-Tr)	**1 S**
Yavmetdinov *et al*. (2003)	Wheat straw	45	*Coriolus hirsutus (Ch)* *Cerrena maxima (Cm)*	53 (Ch) 60 (Cm)	33 (Ch-Cm)	**1 A**
Zhou and Li (2016)	Oat straw	14	*Phanerochaete chrysosporium (Pc)* *Trichoderma viride (Tv)*	35 (Pc) 35 (Tv)	57 (Pc-Tv)	**1 S**

* The nomenclature of the species *C. cinereus, C. hirsutus, C. spinulosum, C. maxima, D. flavida, F. moniliforme, P. chrysosporium, P. guilliermondii, P. palustris, P. rivulosus, P. sajor-caju* and *P. sanguineus* used in the studies correspond to synonyms of current scientific names, which can be consulted at the Index Fungorum online platform.

Synergistic co-cultures

In general, co-cultures are studied for synergistic results, specifically beneficial effects that are not achieved by organisms grown in isolation (Van Dyk and Pletschke, 2012). These synergistic co-cultures with the ability to degrade lignin in an intensified way, in relation to the axenic cultures, are due to the enzymatic synergism resulting from the increase in ligninolytic activities either the positive regulation of constitutive enzymes or the induction of new isoenzymes with different properties (Ramamurthy *et al.*, 2017). Native polyacrylamide gel electrophoresis (native PAGE) (Savoie *et al.*, 1998; Flores *et al.*, 2010; Zhang *et al.*, 2019) or western blot (Chi *et al.*, 2007) are the main analytical methods that confirm enzyme induction in co-cultures.

Enzymatic changes in co-cultures generally followed lignin degradation. The laccase (Lac), lignin peroxidase (LiP), and manganese peroxidase (MnP) activities are reported to be higher in co-cultures than in their respective axenic cultures (Koroleva *et al.*, 2002; Ke *et al*., 2011; Yang *et al.*, 2013; Feng *et al.*, 2015; Tao *et al.*, 2016; Meehnian *et al.*, 2017; Kaur *et al.*, 2018; Xie *et al.*, 2020; Cui *et al.*, 2021). The most expressive result was identified by Meehnian *et al.* (2017) who co-cultivated *Daedalea flavida* and *Phlebia radiata* on cotton stems and obtained 14.2 IU g-1 of laccase activity on the fifteenth day of solid treatment, exceeding three and eight times the axenic cultures, respectively.

However, the enzymatic context should be interpreted with caution since augmentation in ligninolytic activity alone should not be considered responsible for all the lignin degradation identified. Luo *et al.* (2020) observed that the synergistic co-culture of *Irpex lacteus* and *P. chrysosporium* showed a slight decrease in enzymatic activities compared to the respective axenic cultures despite the co-culture presented the highest rate of lignin degradation. Still in the same study, this co-culture was the only one to show the three measured enzymes (Lac, LiP, and MnP). This result indicates that the enzymatic diversity of the system is as relevant as the enzyme expression, as they act on different targets or degradation modes to contribute to lignin degradation.

Ma *et al.* (2011) reported that co-culture of *Auricularia polytricha* and *I. lacteus*, despite showing significantly increased laccase activities than the corresponding axenic cultures did not result in lignin-degrading synergism. Stepanova *et al.* (2003) also reported this lack of correlation between lignin degradation rate and ligninolytic activity.

In these cases, the increase in ligninolytic enzyme expression might have another purpose, not only lignin degradation. Laccase acts in other physiological processes during ecological interactions, such as response to oxidative stress, mycelial invasion, detoxification, mycelial morphogenesis, and melanin pigment production (Baldrian, 2006; Bertrand *et al.*, 2013). The two aforementioned exceptions highlighted the gap in the literature concerning the current knowledge on fungal processes involved in lignin degradation and the sequential role of ligninolytic enzymes during material breakdown and regulation of homeostasis.

Based on the microbial competition by interference and/or exploitation, Hiscox *et al.* (2018) and Ujor *et al.* (2018) reported that the synergistic effect on lignin degradation could be due to the intensified substrate consumption by fungi in the presence of other organisms. This strategy of accelerated substrate colonization might reflect the attempt of one or both fungi to sequester nutrients more rapidly from the interaction zone. It would ensure more nutrient resources for carbon and energy investment in costly antagonistic mechanisms and/or maintenance of the occupied territory, resulting in marked substrate decomposition. Competition theoretically becomes more intense when nutrients are scarce. The ability to degrade lignin, which limits the access to carbohydrates (holocellulose), could benefit the fungus with the highest fitness during these dynamics.

Consumption of resources such as lignin and metabolite deposition by the mycelium is expected to change the microenvironment. These changes could facilitate colonization by other fungi, thus facilitating their coexistence by partitioning the resources according to their metabolic constraints (Boddy and Hiscox, 2016). This niche differentiation motivated researchers to co-culture white-rot fungi with soft-rot fungi (Ke *et al.*, 2011; Darwish *et al.*, 2012; Feng *et al.*, 2015, 2016) or with yeasts (Yang *et al.*, 2013; Cui *et al.*, 2015; Tao *et al.*, 2016; Zhou and Li, 2016). Both soft-rot fungi and yeasts can hydrolyze holocellulosic portions more intensively, making sugars available to white-rot fungi. In compensation, white-rot fungi reduce substrate recalcitrance, creating a cocktail of local enzymes that can theoretically degrade all lignocellulose components.

Secondary analytical methods, such as Scanning Electron Microscopy (SEM), are used to confirm lignin degradation (Gamal *et al.*, 2014; Feng *et al.*, 2015; Zhou and Li, 2016; Meehnian *et al.*, 2017; Kaur *et al.*, 2018; Luo *et al.*, 2020; Cui *et al.*, 2021; Fatma *et al.*, 2021; Li *et al.*, 2021) and concluded that different co-cultures can accentuate plant cell wall degradation. The action of the fungi in the co-culture changed the initially smooth surface into an irregular surface material, with greater exposure to cellulose fibers, which can collapse, resulting in a flatter structure. In addition, SEM images showed the destruction of non-lignocellulosic structural components (papillae and phytoliths) and the enlargement of substrate porosity to facilitate the penetration of hyphae and other enzymes. Luo *et al.* (2020) observed on electron micrographs enhanced lignin degradation (a 3 % increase in the distribution of pores larger than 10,000 nm in diameter) in co-cultures of *I. lacteus* and *P. chrysosporium* incubated in alkaline lignin for 21 days compared to the respective axenic cultures.

Finally, despite the clear benefits of co-culture relative to axenic cultures, monitoring fungal interactions during incubation is essential to confirm synergism stability. Due to instabilities related to initial microenvironmental modifications or species competitiveness, reproducibility of co-culture results is challenging (Woodward and Boddy, 2008).

Antagonistic co-cultures

The antagonistic co-cultures are characterized by less lignin degradation in the co-cultures than in the respective axenic cultures. These cultures are the most suitable systems for understanding incompatibilities that have not yet been fully clarified. The antagonistic effect seems not to be directly related to the fungal groups co-cultured, as antagonistic co-cultures of aero-aquatics ascomycetes (Bergbauer *et al.*, 1992), yeasts (Qadir *et al.*, 2018) and even white-rot fungi (Yavmetdinov *et al.*, 2003; Wang *et al.*, 2014; Kaur *et al.*, 2018) have been reported.

In accordance with Bergbauer *et al.* (1992), the most plausible explanation for the incompatibility could be the inhibitory effect arising from antimicrobial compounds produced as result of the microorganism's interaction. Although they did not perform measurements, the mixed cultures of five paired fungi exhibited lower fungal growth and substrate degradation compared to the five respective axenic cultures. Fungal antagonism due to chemical compounds is a very investigated phenomenon, especially in identifying potential antimicrobial drugs using co-cultures of terrestrial filamentous fungi (Bertrand *et al.*, 2014; Abdalla *et al.*, 2017; Arora *et al.*, 2020). In addition, it might also be a possible explanation for the results observed with white-rot fungi co-cultures (Evans *et al.*, 2008; Yao *et al.*, 2016; Zhong *et al.*, 2019).

Other mechanisms underlying ecological interactions could be responsible for reducing the ability of these fungi. Some strategies can dislocate part of the free metabolic energy to the execution of antagonistic mechanisms to the detriment of lignin degradation. For example, the intensified mycoparasitism or oxidative stress, physiomorphological changes for resistance to invasion or induction of mycelial substitution, and competition for the substrate that causes nutrient depletion are some of these factors (Hiscox and Boddy, 2017; Hiscox *et al.*, 2018).

The antagonism between *Candida tropicalis* and *Saccharomyces cerevisiae* yeasts in co-culture by Qadir *et al.* (2018) represents a scientific gap in the metabolic pathways and ligninolytic potential of these fermenters, which needs further investigation (Košíková and Sláviková, 1996; Larroy *et al.*, 2003; Yang *et al.*, 2017). However, this antagonistic effect could be due to the antifungal compound released by *S. cerevisiae* during co-culture (Albergaria *et al.*, 2010; Fakruddin *et al.*, 2017) and/or to the toxicity effect of the lignin itself and its derivatives on the yeast (Dong *et al*., 2011; García *et al.*, 2017; Gu *et al.*, 2019), but further experimental confirmation is needed.

Although yeasts have a low ligninolytic potential, Wang *et al.* (2015) using scanning microscopy observed that the co-culture of *Rhodotorula mucilaginosa* and *Pleurotus ferulae* had intercellular communications, responsible for the synergistic increase in laccase activity. Laccase is released by the filamentous fungus when stimulated by the yeast. Even though this study did not approach lignin degradation, it showed that the feasibility of applying yeasts for degradation depends on the co-culture performed.

The low frequency reported of antagonism in co-cultures could be due to the efficient selection of species with high biotechnological potential by researchers or the tendency of scientific journals not to publish negative results (Fanelli, 2010; Silva, 2015). In general, the chemical antagonism resulting from competition is

well studied in antagonistic co-cultures, however, more attention to the degradative context is required to elucidate the factors causing lower ligninolytic performance in antagonistic co-cultures.

Neutral co-cultures

Neutral co-cultures are the most frequently identified. They exhibit an intermediate lignin degradation rate relative to axenic cultures or no significant difference compared to at least one of the axenic cultures, resulting in a neutral performance. This neutrality is not yet well understood and might be due to several factors. Among them, we can list: the balance between antagonistic and synergistic effects, the species coexistence, the absence of ecological interaction or recognition of another organism, the predominance of the most combative species, the interaction resulting in synergism or antagonism for a single specie (Boddy, 2000; Boddy and Hiscox, 2016; Hiscox and Boddy, 2017; Hiscox *et al.*, 2018) and even a short incubation period of the system (Kuhar *et al.*, 2015).

Co-cultures with intermediate rates of lignin degradation relative to the respective axenic culture are limited by interspecific resource competition. In some cases, they can be elucidated by the predominance of fungal degradative metabolism with a more combative potential, capable of hindering the stabilization of the less aggressive competitor, especially if it is a co-culture of different groups of rot fungi. Hermosilla *et al.* (2018) co-cultured *Ganoderma lobatum* (a white-rot fungus) and *Gloeophyllum trabeum* (a brown-rot fungus) and found that the latter predominated in the system through cell lysis mechanisms. Consequently, it reduced the growth of the white-rot fungus, which was reflected in lower lignin degradation potentials in co-culture than expected in axenic cultures of the white-rot fungus.

Arora (1995) analyzed the degradation efficiency of different ecological groups of rot fungi, comparing combinations of two brown-rot fungi or two soft-rot fungi under the same experimental conditions. He found a non-significant lignin degradation relative to axenic cultures. The only culture systems with significant differences in ligninolytic potential were the co-cultures between white-rot fungi with fungi of any other type of rot, i.e. white, soft or brown-rot fungi. Sundman and Näse (1972) co-cultured fungi from different ecological groups and found a similar pattern, although the interaction mechanisms and overlapping effects of decay metabolism remain uncertain.

Although commensalism and amensalism have been little explored in mycology, they appear to be plausible hypotheses for most neutral co-cultures. In this context, Giles *et al*. (2014) co-cultured *Ceriporiopsis subvermispora* and *Pleurotus ostreatus* and found no synergistic or antagonistic interaction. Subsequently, these authors identified mutual antagonistic inhibition between *C. subvermispora* and *Postia placenta* in co-cultures (Giles *et al.*, 2015). However, the absence of interaction or antagonism in both cases did not lead to any statistically significant difference in lignin degradation between the co-cultures and the respective axenic cultures.

The results obtained by Chi *et al.* (2007) emphasized the importance of the combination of species and the microenvironmental conditions of the system (substrate, fermentation mode, temperature, pH, among others) as relevant variables to determine the interaction. These authors reported the synergistic production of ligninolytic enzymes evidenced by a qualitative discoloration of the polymeric dye Poly R-478 and the stimulation of new isoenzymes in the co-culture of *C. subvermispora* and *P. ostreatus*, compared to axenic cultures. However, the co-culture did not significantly decrease the lignin content in poplar wood after two to six weeks of incubation compared to axenic cultures. Kuhar *et al.* (2015) obtained similar results in an incubation period of only two weeks.

In all the above situations, specific monitoring of the dynamics of ecological interactions between cultured organisms is needed to understand the factors involved in decreasing lignin content in neutral co-cultures.

Instability of co-cultures

Lack of reproducibility is one of the main challenges in large-scale co-cultivation because the dynamics of the interactions can vary with minor changes in the system (Huisman and Weissing, 2001; Goers *et al.*, 2014; Arora *et al.*, 2020). This drawback can also be observed in prospective co-cultures for lignin degradation.

No changes were observed in the co-culture degradative profile if the initial conditions were slightly altered (Table 1). For example, Carabajal *et al.* (2012) performed three mushroom co-cultures in bags with wheat straw. They inoculated *P. ostreatus* in the upper part of the bag and *P. citrinopileatus* in the lower part (PO/PC). In addition, they carried out the reverse distribution (PC/PO) and a homogeneous mixture of both (PO+PC). Still, all resulted in neutral co-cultures relative to the respective axenic cultures. Song *et al.* (2012) found similar results while co-cultivating *G. trabeum* and *I. lacteus* in three distinct wood types. On the other hand, Darwish *et al.* (2012) co-cultured *P. ostreatus* with three different amounts of *S. cerevisiae* inoculum (15, 30, and 45 mL) and found enhanced lignin degradation compared to the corresponding axenic cultures. The co-culture of *P. chrysosporium* and *Lentinus tigrinus* showed a similar synergism pattern varying only the strain (M6 or RO2) of the latter specie Jamal *et al.* (2015).

However, the other co-cultures with the same species combination made by different authors, showed divergent results in lignin degradation. For example, the co-culture of *P. ostreatus* and *P. chrysosporium* on poplar wood (Chi *et al*., 2007) or rice straw (Kaur *et al*., 2018) resulted in neutral or synergistic co-cultures, respectively. Similar results were found in co-cultures of *P. ostreatus* and *C. subvermispora* (Chi *et al.*, 2007; Giles *et al.*, 2014; Xie *et al.*, 2020) and *P. chrysosporium* and *T. viride* (Tao *et al.*, 2016; Zhou and Li, 2016; Sasongko *et al.*, 2019). Only the combination of *C. hirsutus* and *C. maxima* grown under sulfonated lignin (Koroleva *et al.*, 2002) or on oat straw (Yavmetdinov *et al.*, 2003) resulted in a synergistic and antagonistic pattern, respectively.

These findings demonstrated that a single modification in the replicate co-cultures is not enough to change the lignin degradation profile. However, a set of changes in culture conditions (like substrate, culture type and mode, temperature, fermentation state, and other variables) can change the degradative profile of these systems by affecting the development of interactions (Huisman and Weissing, 2001; Goers *et al.*, 2014; Arora *et al.*, 2020).

The optimal approach to understanding the dynamics of substrate degradation is to measure lignin degradation over more than one day of incubation, either by destructive or non-destructive sampling. It can also identify whether the co-culture potential for lignin degradation is constant (Bergbauer *et al.*, 1992; Carvalheiro *et al.*, 1994; Chi *et al.*, 2007; Albert and Pandya, 2013; Nazarpour *et al.*, 2013; Yang *et al.*, 2013; Gamal *et al.*, 2014; Wang *et al.*, 2014; Chen *et al.*, 2015; Feng *et al.*, 2015, 2016; Zhou and Li, 2016; Meehnian *et al.*, 2017; Xie *et al.*, 2020) or fluctuating (Ke *et al.*, 2011; Ma *et al.*, 2011; Yang *et al.*, 2011; Darwish *et al.*, 2012; Luo *et al.*, 2020) relative to axenic cultures over the culture incubation time.

In situations where the degradation potential of the co-cultures fluctuated during incubation, consecutive sampling provided evidence that the co-culture could initially be characterized in one group and changed to another profile during incubation. Ma *et al.* (2011) reported that the co-culture analyzed showed a higher rate of lignin degradation during the initial incubation period (5, 10, and 15 days) but did not differ statistically from one of the axenic cultures after 20 to 25 days. Other studies (Yang *et al.*, 2011; Darwish *et al.*, 2012) showed similar fluctuations. Reverse results in which co-cultures were initially classified as neutral and then increased the lignin degradation relative to axenic cultures have also been identified (Ke *et al.*, 2011; Luo *et al.*, 2020). However, no changes related to the antagonistic profile were observed.

Therefore, the absence of additional sampling would result in partial inferences of the real properties of co-cultures. However, even though additional sampling is recommended, the instability of ecological interactions throughout cultivation and the scarcity of measurement resources could limit obtaining the data necessary for this type of monitoring.

Biotechnological applications

The ability of fungal co-cultures to degrade lignin can be harnessed for biotechnological uses in which the decrease in the recalcitrance of this polymer is sought. The application of fungi in the sustainable pretreatment of second-generation lignocellulose in biorefineries aims to shorten the incubation time and lignin removal efficiency. These innovations in the process have made this alternative competitive against the chemical and/or physical methods adopted (Bader *et al.*, 2010). In addition, fungal co-culture is also promising in downstreaming of fermentable sugar biorefinery for the generation of different biofuels (Jiang *et al.*, 2017) and lignin depolymerization for the generation of high-value-added chemicals, especially lignin-derived aromatic compounds (Asina *et al.*, 2017; Arora *et al.*, 2018).

The same is valid for the production of animal feed for ruminants by the biotreatment of lignocellulosic agricultural residues with white-rot fungi. Lignin reduction facilitates palatability, digestibility, and increase the crude protein content of the material (Sharma and Arora, 2013), resulting in better nutritional quality feeds. Co-culture studies have already reported obtaining higher nutritional quality feeds than axenic cultures (Asiegbu *et al.*, 1996; Ke *et al.*, 2011; Darwish *et al.*, 2012; Jamal *et al.*, 2015; Tao *et al.*, 2016), indicating the potential application of co-cultures in this industry.

White-rot fungi also show promising results for preferential lignin degradation in biopulping, a sustainable alternative compared to traditional chemical and/or mechanical methods (Singh *et al.*, 2010; Kumar *et al.*, 2020). *Ceriporiopsis subvermispora* seems to be the most suitable species for bleaching processes. Its co-culture with *Ophiostoma piliferum* could result in an additional decrease in the kappa number and better-quality properties of the paper (Gamal *et al.*, 2014). However, *C. subvermispora* co-cultured with *Physisporinus rivulosus* or *P. ostreatus* showed no significant difference in delignification compared with axenic cultures (Chi *et al.*, 2007). Therefore, as mentioned above, this species can be combined with compatible organisms to synergize and improve desired aspects.

The ligninolytic enzymes of white-rot fungi, especially laccase, can degrade xenobiotics due to the nonspecific action, which can efficiently detoxify the environment. Consequently, effluents from the pulp and paper industry, soils contaminated with pesticides and wastewater generated by the textile industry, distillery and other sectors that discharge aromatic residues into the environment are susceptible to fungal bioremediation (Asgher *et al.*, 2008; Ijoma and Tekere, 2017). In one study, Kuhar *et al.* (2015) co-cultured *Ganoderma lucidum* and *Trametes versicolor* and did not obtain synergistic lignin degradation. However, this system improved the *in vitro* degradation of malachite green dye compared to the isolated cultures.

On the other hand, co-culture application in the production of edible mushrooms is based on the assumption of displacement of fungal secondary metabolism as a result of ecological interactions. Thus, the time required for forming basidiomes is reduced, allowing the simultaneous production of different edible species in the same bag. However, only Carabajal *et al.* (2012) tested this assumption by co-cultivating *P. ostreatus* and *P. citrinopileatus*. They found that co-culture did not increase basidiome production; instead, it inhibited *P. ostreatus* development and basidiome stem's length decreased significantly. Further research with other edible fungi is needed to clarify the biotechnological feasibility of this technique.

Other widely investigated technique is the composting, especially as an alternative for the final disposal of lignocellulosic agricultural residues that accumulate on farms without further treatment or are ultimately burned with the consequent production of greenhouse gases. Unexpectedly, Yavmetdinov *et al.* (2003) observed a lower lignin degradability in an *in vitro* co-culture on oat straw, while humin-like substances (desirable in composting) were increased compared to the respective axenic cultures.

Given this scenario, the gradual use and foreseeable applicability of fungal co-cultures have a promising future. However, its biotechnological implementation

will pose challenges unforeseen at the laboratory scale, such as difficult operational control and stabilization of co-cultures during fermentation in large proportions. Thus, further studies, mainly focused on industrial adaptation and optimization are needed to ensure the benefits of this cultivation technique. Furthermore, new microorganisms must be prospected as well as pairs of previously untested species to obtain new co-cultures capable of better degrading of lignin than the individual organisms (Singh and Singh, 2014).

CONCLUSION

Fungal co-cultures, which simulate fungal ecological interactions in ecosystems, have been shown to potentially increase the efficiency of lignocellulose degradation, particularly the lignin polymer, due to enhanced ligninolytic activity. Co-cultures with neutral or synergistic effects are more frequent than those with antagonistic effects. The selection of species to be co-cultured and the environmental conditions of the system are determining factors for the outcome of the interaction, although the underlying mechanisms are still being elucidated. In general, the variability of lignin degradation in a given co-culture will depend directly on the inhibitory effects of competition or the stimulating effects of compatibility and beneficial physiological changes. Pairing tests with promising species under various environmental conditions are essential to identify the combination that best meets the desired goals. Finally, this review demonstrates the promising applicability of fungal co-cultures in different biotechnological sectors to increase the degradation of lignin and its derivatives. This trend requires the confirmation of further studies on ecological and industrial scales, intending to make the most of the co-culture potential.

ACKNOWLEDGMENTS

The authors thank CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for the financial support, IPA (Instituto de Pesquisas Ambientais) and UNIFESP (Universidade Federal de São Paulo).

BIBLIOGRAPHY

Abdalla, M. A., Sulieman, S. & McGaw, L. J. (2017). Microbial communication: A significant approach for new leads. *South African Journal of Botany 113*: 461-470. doi: 10.1016/j.sajb.2017.10.001

Abdel-Hamid, A. M., Solbiati, J. O. & Caan, I. K. O. (2013). Insights into lignin degradation and its potential industrial applications. *Advances in Applied Microbiology 82*: 1-28. doi: 10.1016/B978-0-12-407679-2.00001-6

Adav, S. S., Ravindran, A., Cheow, E. S. H. & Sze, S. K. (2012). Quantitative proteomic analysis of secretome of microbial consortium during saw dust utilization. *Journal of Proteomics 75* (18): 5590-5603. doi: 10.1016/j.jprot.2012.08.011

Albergaria, H., Francisco, D., Gori, K., Arneborg, N. & Gíria, F. (2010). *Saccharomyces cerevisiae* CCMI 885 secretes peptides that inhibit the growth of some non-*Saccharomyces* wine-related strains. *Applied Microbiology and Biotechnology 86*: 965-972. doi: 10.1007/s00253-009-2409-6

Albert, S. & Pandya, B. (2013). Pattern of bamboo culm degradation by *Daedaleopsis confragosa* when co-cultured with selected fungi. *Annals of Plant Sciences 2* (12): 563-574.

Arfi, Y., Levasseur, A. & Record, E. (2013). Differential gene expression in *Pycnoporus coccineus* during interspecific mycelial interactions with different competitors. *Applied and Environmental Microbiology 79* (21): 6626-6636. doi: 10.1128/AEM.02316-13

Arora, D. S. (1995). Biodelignification of wheat straw by different fungal associations. *Biodegradation 6* (1): 57-60.

Arora, D., Gupta, P., Jaglan, S., Roullier, C., Grovel, O. & Bertrand, S. (2020). Expanding the chemical diversity through microorganisms co-culture: Current status and outlook. *Biotechnology Advances 40*: 1-14. doi: 10.1016/j.biotechadv.2020.107521

Arora, R., Sharma, N. K. & Kumar, S. (2018). Chapter 8 - Valorization of by-products following the biorefinery concept: commercial aspects of by-products of lignocellulosic biomass. *Technologies, Commercialization, Policy Issues and Paradigm Shift for Bioethanol and By-Products* 163-178. doi: 10.1016/B978-0-12-804534-3.00008-2

Asgher, M., Bhatti, H. N., Ashraf, M. & Legge, R. L. (2008). Recent developments in biodegradation of industrial pollutants by white rot fungi and their enzyme system. *Biodegradation 19*: 771-783. doi: 10.1007/s10532-008-9185-3

Asiegbu, F. O., Paterson, A. & Smith, J. E. (1996). The effects of co-fungal cultures and supplementation with carbohydrate adjuncts on lignin biodegradation and substrate digestibility. *World Journal of Microbiology and Biotechnology 12*: 273-279. doi: 10.1007/BF00360927

Asina, F., Brzonova, I., Kozliak, E., Kubátová, A. & Ji, Y. (2017). Microbial treatment of industrial lignin: Successes, problems and challenges. *Renewable and Sustainable Energy Reviews 77*: 1179-1205. doi: 10.1016/j.rser.2017.03.098

Bader, J., Mast-Gerlach, E., Popovic, M. K., Bajpai, R. & Stahl, U. (2010). Relevance of microbial co culture fermentations in biotechnology. *Journal of Applied Microbiology 109*: 371-387. doi: 10.1111/j.1365-2672.2009.04659.x

Baldrian, P. (2006). Fungal laccases – occurrence and properties. *FEMS Microbiology Reviews 30* (2): 215-242. doi: 10.1111/j.1574-4976.2005.00010.x

Becker, J. & Wittmann, C. (2019). A field of dreams: Lignin valorization into chemicals, materials, fuels, and health-care products. *Biotechnology Advances 37* (6): 1-24. doi: 10.1016/j.biotechadv.2019.02.016

Bergbauer, M., Moran, M. A. & Hodson, R. E. (1992). Decomposition of lignocellulose from a freshwater macrophyte by aero-aquatic fungi. *Microbial Ecology 23*: 159-167. doi: 10.1007/BF00172637

Bertrand, B., Martínez-Morales, F. & Trejo-Hernández, M. R. (2013). Fungal laccases: induction and production. *Revista Mexicana de Ingeniería Química 12* (3): 473-488.

Bertrand, S., Bohni, N., Schnee, S., Schumpp, O., Gindro, K. & Wolfender, J. (2014). Metabolite induction via microorganism co-culture: A potential way to enhance chemical diversity for drug discovery. *Biotechnology Advances 32* (6): 1180-1204. doi: 10.1016/j.biotechadv.2014.03.001

Bertrand, S., Schumpp, O., Bohni, N., Bujard, A., Azzollini, A., Monod, M., Gindro, K. & Wolfender, J. (2013a). Detection of metabolite induction in fungal co-cultures on solid media by high-throughput differential ultra-high pressure liquid chromatography–time-of-flight mass spectrometry fingerprinting. *Journal of Chromatography A 1292*: 219-228. doi: 10.1016/j.chroma.2013.01.098

Bertrand, S., Schumpp, O., Bohni, N., Bujard, A., Monod, M., Gindro, K. & Wolfender, J. (2013b). De Novo production of metabolites by fungal co-culture of *Trichophyton rubrum* and *Bionectria ochroleuca*. *Journal of Natural Products 76* (6): 1157-1165. doi: 10.1021/np400258f

Boddy, L., Owens, E. M. & Chapela, I. H. (1989).Small scale variation in decay rate within logs one year after felling: Effect of fungal community structure and moisture content. *FEMS Microbiology Ecology 5* (3): 173-183. doi: 10.1111/j.1574-6968.1989.tb03691.x

Boddy, L. (2000). Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS Microbiology Ecology 31* (3): 185-194. doi: 10.1111/j.1574-6941.2000.tb00683.x

Boddy, L. & Hiscox, J. (2016). Fungal ecology: Principles and mechanisms of colonization and competition by saprotrophic fungi. *Microbiology Spectrum 4* (6): 1-16. doi: 10.1128/microbiolspec.FUNK-0019-2016

Carabajal, M., Levin, L., Albertó, E. & Lechner, B. (2012). Effect of co-cultivation of two *Pleurotus* species on lignocellulolytic enzyme production and mushroom fructification. *International Biodeterioration & Biodegradation 66* (1): 71-76. doi: 10.1016/j.ibiod.2011.11.002

Carvalheiro, F., Roseiro, J. C. & Collaço, M. T. A. (1994). Biological conversion of tomato pomace by pure and mixed fungal cultures. *Process Biochemistry 29* (7): 601-605. doi: 10.1016/0032-9592(94)80025-1

Chen, H. (2014). Chapter 2 Chemical composition and structure of natural lignocellulose. Biotechnology of lignocellulose: Theory and Practice. Beijing, China: Chemical Industry Press 1-47. doi: 10.1007/978-94-007-6898-7_2

Chen, Y., Huang, J., Li, Y., Zeng, G., Zhang, J., Huang, A., Zhang, J., Ma, S., Tan, X., Xu, W. & Zhou, W. (2015). Study of the rice straw biodegradation in mixed culture of *Trichoderma viride* and *Aspergillus niger* by GC-MS and FTIR. *Environmental Science and Pollution Research 22*: 9807-9815. doi: 10.1007/s11356-015-4149-8

Chi, Y., Hatakka, A. & Maijala, P. (2007). Can co-culturing of two white-rot fungi increase lignin degradation and the production of lignin-degrading enzymes?. *International Biodeterioration & Biodegradation 59* (1): 32-39. doi: 10.1016/j.ibiod.2006.06.025

Chio, C., Sain, M. & Qin, W. (2019). Lignin utilization: A review of lignin depolymerization from various aspects. *Renewable and Sustainable Energy Reviews 107*: 232-249. doi: 10.1016/j.rser.2019.03.008

Cui, T., Yuan, B., Guo, H., Tian, H., Wang, W., Ma, Y., Li, C. & Fei, Q. (2021). Enhanced lignin biodegradation by consortium of white rot fungi: microbial synergistic effects and product mapping. *Biotechnology for Biofuels 14* (162): 1-11. doi: 10.1186/s13068-021-02011-y

Cui, Y., Dong, X., Tong, J. & Liu, S. (2015). Degradation of lignocellulosic components in un-pretreated vinegar residue using an artificially constructed fungal consortium. *BioResources 10* (2): 3434-3450. doi: 10.15376/biores.10.2.3434-3450

Darwish, G. A. M. A., Bakr, A. A. & Abdallah, M. M. F. (2012). Nutritional value upgrading of maize stalk by using *Pleurotus ostreatus* and *Saccharomyces cerevisiae* in solid state fermentation. *Annals of Agricultural Sciences 57* (1): 47-51. doi: 10.1016/j.aoas.2012.03.005

Dashtban, M., Schraft, H., Syed, T. A. & Qin, W. (2010). Fungal biodegradation and enzymatic modification of lignin. *International Journal of Biochemistry and Molecular Biology 1* (1): 36-50.

Dong, X., Dong, M., Lu, Y., Turley, A., Jin, T. & Wu, C. (2011). Antimicrobial and antioxidant activities of lignin from residue of corn stover to ethanol production. *Industrial Crops and Products 34* (3): 1629-1634. doi: 10.1016/j.indcrop.2011.06.002

Dullah, S., Hazarika, D. J., Parveen, A., Kakoti, M., Borgohain, T., Gautom, T., Bhattacharyya, A., Barooah, M. & Boro, R. C. (2021). Fungal interactions induce changes in hyphal morphology and enzyme production. *Mycology: An International Journal on Fungal Biology 12* (1): 279-295. doi: 10.1080/21501203.2021.1932627

Evans, J. A., Eyre, C. A., Rogers, H. J., Boddy, L. & Muller, C. T. (2008). Changes in volatile production during interspecific interactions between four wood rotting fungi growing in artificial media. *Fungal Ecology 1* (2-3): 57-68. doi: 10.1016/j.funeco.2008.06.001

Ezeonu, C. S., Onwurah, I. N. E., Ubani, C. S., Ejikeme, C. M. & Ogodo, A. C. (2016). *Trichophyton soudanense* and *Trichophyton mentagrophyte* - treated rice husk biomass components and effect of yeast on the bioethanol yield. *Achievements in the Life Sciences 10* (1): 72-79. doi: 10.1016/j.als.2016.05.007

Fakruddin, M., Hossain, M. N. & Ahmed, M. M. (2017). Antimicrobial and antioxidant activities of *Saccharomyces cerevisiae* IFST062013, a potential probiotic. *BMC Complementary and Alternative Medicine 17* (64): 1-11. doi: 10.1186/s12906-017-1591-9

Fanelli, D. (2010). Do pressures to publish increase scientists' bias? An empirical support from US states data. *PLOS ONE 5* (4): 1-7. doi: 10.1371/journal.pone.0010271

Fatma, S., Saleem, A. & Tabassum, R. (2021). Wheat straw hydrolysis by using co-cultures of *Trichoderma reesei* and *Monascus purpureus* toward enhanced bio-

degradation of the lignocellulosic biomass in bioethanol biorefinery. *Biomass Conversion and Biorefinery 11*: 743-754. doi: 10.1007/s13399-020-00652-x

Feng, N., Ma, Q., Yuan, M., Zhai, H. & Ek, M. (2015). Improving degradation ability toward wheat straw chemical composition by co-cultivation of *Pycnoporus sanguineus* with *Candida tropicalis*. *Journal of Biobased Materials and Bioenergy 9* (6): 567-571. doi: 10.1166/jbmb.2015.1555

Feng, N., Zhai, H. & Lai, Y. (2016). On the chemical aspects of the biodelignification of wheat straw with *Pycnoporus sanguineus* and its combined effects with the presence of *Candida tropicalis*. *Industrial Crops and Products 91*: 315-322. doi: 10.1016/j.indcrop.2016.07.035

Flores, C., Casasanero, R., Trejo-Hernández, M. R., Galindo, E. & Serrano-Carreón, L. (2010). Production of laccases by *Pleurotus ostreatus* in submerged fermentation in co-culture with *Trichoderma viride*. *Journal of Applied Microbiology 108* (3): 810-817. doi: 10.1111/j.1365-2672.2009.04493.x

Gamal, R. F., Abdelhady, H. M., Nageeb, Z. A. & Elgarhy, E. A. (2014). Pulping of sugarcane bagasse using *Ceriporiopsis subvermispora* SS-33 and *Ophiostoma piliferum* as a fungal bio-agents. *Egyptian Journal of Microbiology 49* (1): 1-15. doi: 10.21608/EJM.2014.239

García, A., Spigno, G. & Labidi, J. (2017). Antioxidant and biocide behavior of lignin fractions from apple tree pruning residues. *Industrial Crops and Products 104*: 242-252. doi: 10.1016/j.indcrop.2017.04.063

Giles, R. L., Galloway, E. R., Zackeru, J. C., Naithani, V. & Parrow, M. W. (2014). Two stage fungal biopulping solubilizes lignocellulosic carbohydrates without supplemental enzymatic hydrolysis. *International Biodeterioration & Biodegradation 86*: 265-271. doi: 10.1016/j.ibiod.2013.09.016

Giles, R. L., Zackeru, J. C., Galloway, E. R., Elliott, G. D. & Parrow, M. W. (2015). Single *versus* simultaneous species treatment of wood with *Ceriporiopsis subvermispora* and *Postia placenta* for ethanol applications, with observations on interspecific growth inhibition. *International Biodeterioration & Biodegradation 99*: 66-72. doi: 10.1016/j.ibiod.2014.11.005

Goers, L., Freemont, P. & Polizzi, M. (2014). Co-culture systems and technologies: taking synthetic biology to the next level. *Journal of the Royal Society Interface 11* (96): 1-13. doi: 10.1098/rsif.2014.0065

Gu, H., Zhu, Y., Peng, Y., Liang, X., Liu, X., Shao, L., Xu, Y., Xu, Z., Liu, R. & Li, J. (2019). Physiological mechanism of improved tolerance of *Saccharomyces cerevisiae* to lignin-derived phenolic acids in lignocellulosic ethanol fermentation by short-term adaptation. *Biotechnology for Biofuels 12* (268): 1-14. doi: 10.1186/s13068-019-1610-9

Guerriero, G., Hausman, J., Strauss, J., Ertan, H. & Siddiqui, K. S. (2016). Lignocellulosic biomass: Biosynthesis, degradation, and industrial utilization. *Engineering in Life Sciences 16*: 1-16. doi: 10.1002/elsc.201400196

Hermosilla, E., Rubilar, O., Schalchli, H., Silva, A. S., Ferreira-Leitao, V. & Cristina Diez, M. (2018). Sequential white-rot and brown-rot fungal pretreatment of wheat straw as a promising alternative for complementary mild treatments. *Waste Management 79*: 240-250. doi: 10.1016/j.wasman.2018.07.044

Hiscox, J. & Boddy, L. (2017). Armed and dangerous - Chemical warfare in wood decay communities. *Fungal Biology Reviews 31* (4): 169-184. doi: 10.1016/j.fbr.2017.07.001

Hiscox, J., O'leary, J. & Boddy, L. (2018). Fungus wars: basidiomycete battles in wood decay. *Studies in Mycology 89*: 117-124. doi: 10.1016/j.simyco.2018.02.003

Holmer, L. & Stenlid, J. (1993). The importance of inoculum size for the competitive ability of wood decomposing fungi. *FEMS Microbiology Ecology 12* (3): 169-176. doi: 10.1111/j.1574-6941.1993.tb00029.x

Horsley, T., Dingwall, O. & Sampson, M. (2011). Checking reference lists to find additional studies for systematic reviews. *Cochrane Database of Systematic Reviews 8*: 1-27. doi: 10.1002/14651858.MR000026.pub2

Huisman, J. & Weissing, F. J. (2001). Fundamental unpredictability in multispecies competition. *The American Naturalist 157* (5): 488-494. doi: 10.1086/319929

Iakovlev, A. & Stenlid, J. (2000). Spatiotemporal patterns of laccase activity in interacting mycelia of wood-decaying basidiomycete fungi. *Microbial Ecology 39* (3): 236-245. doi: 10.1007/s002480000022

Ijoma, G. N. & Tekere, M. (2017). Potential microbial applications of co-cultures involving ligninolytic fungi in the bioremediation of recalcitrant xenobiotic compounds. *International Journal of Environmental Science and Technology 14*: 1787-1806. doi: 10.1007/s13762-017-1269-3

Jamal, P., Saheed, O. K., Karim, M. I. A., Alam, M. Z. & Muyibi, S. A. (2015). A fermentative approach to ameliorating solid waste challenges within food and hospitality industry. *International Biodeterioration & Biodegradation 102*: 182-190. doi: 10.1016/j.ibiod.2015.03.031

Jiang, L., Zhou, J., Quan, C. & Xiu, Z. (2017). Advances in industrial microbiome based on microbial consortium for biorefinery. *Bioresour Bioprocess 4* (11): 1-10. doi: 10.1186/s40643-017-0141-0

Karpe, A. V., Beale, D. J., Harding, I. H. & Palombo, E. A. (2014). Optimization of degradation of winery-derived biomass waste by Ascomycetes. *Chemical Technology and Biotechnology 90* (10): 1793-1801. doi: 10.1002/jctb.4486

Kaur, P., Kocher, G. S. & Taggar, M. S. (2018). Development of fungal consortium for the pretreatment of rice straw under optimized solid state and shake flask conditions. *Environmental Progress & Sustainable Energy 38* (2): 635-646. doi: 10.1002/ep.12954

Ke, L., Wu, Q. & Zhang, D. (2011). Bioconversion of rape straw into a nutritionally enriched substrate by *Ganoderma lucidum* and yeast. *African Journal of Biotechnology 10* (29): 5648-5653.

Koroleva, O. V., Gavrilov, V. P., Stepanova, E. V., Lebedeva, V. I., Sverdlova, N. I., Landesman, E. O., Yavmetdinov, I. S. & Yaropolov, A. I. (2002). Production of lignin modifying enzymes by co-cultivated white-rot fungi *Cerrena maxima* and *Coriolus hirsutus* and characterization of laccase from *Cerrena maxima*. *Enzyme and Microbial Technology 30* (4): 573-580. doi: 10.1016/S0141-0229(02)00021-2

Košíková, B. & Sláviková, E. (1996). Growth of *Saccharomyces cerevisiae*, *Rhodotorula rubra* and *Bullera alba* in the presence of beechwood prehydrolyzate-based lignin fractions. *Folia Microbiologica 41*: 430–432. doi: 10.1007/BF02815694

Kuhar, F., Castiglia, V. & Levin, L. (2015). Enhancement of laccase production and malachite green decolorization by co-culturing *Ganoderma lucidum* and *Trametes versicolor* in solid-state fermentation. *International Biodeterioration & Biodegradation 104*: 238-243. doi: 10.1016/j.ibiod.2015.06.017

Kumar, A., Gautam, A. & Dutt, D. (2020). Bio-pulping: An energy saving and environment-friendly approach. *Physical Sciences Reviews 5* (10): 1-9. doi: 10.1515/psr-2019-0043

Larroy, C., Fernández, M. R., González, E., Parés, X. & Biosca, J. A. (2003). Properties and functional significance of *Saccharomyces cerevisiae* ADHVI. *Chemico-Biological Interactions 143-144*: 229-238. doi: 10.1016/s0009-2797(02)00166-7

Li, M., Wang, Z., Sun, J., Chen, W., Hou, X. & Gao, Z. (2021). Synergistic effect of mixed fungal pretreatment on thermogravimetric characteristics of rice straw. *BioResources 16* (2): 3978-3990. doi: 10.15376/biores.16.2.3978-3990

Lundell, T. K., Mäkelä, M. R., Vries, R. P. & Hildén, K. S. (2014). Chapter 11 – Genomics, lifestyles and future prospects of wood-decay and litter-decomposing Basidiomycota. *Advances in Botanical Research 70*: 329-370. doi: 10.1016/B978-0-12-397940-7.00011-2

Luo, R., Liao, Q., Xia, A., Deng, Z., Huang, Y., Zhu, X. & Zhu, X. (2020). Synergistic treatment of alkali lignin via fungal coculture for biofuel production: Comparison of physicochemical properties and adsorption of enzymes used as catalysts. *Frontiers in Energy Research 8* (575371): 1-10. doi: 10.3389/fenrg.2020.575371

Ma, F., Wang, J., Zeng, Y., Yu, H., Yang, Y. & Zhang, X. (2011). Influence of the co-fungal treatment with two white rot fungi on the lignocellulosic degradation and thermogravimetry of corn stover. *Process Biochemistry 46* (9): 1767-1773. doi: 10.1016/j.procbio.2011.05.020

Meehnian, H., Jana, A. K. & Jana, M. M. (2017). Pretreatment of cotton stalks by synergistic interaction of *Daedalea flavida* and *Phlebia radiata* in co-culture for improvement in delignification and saccharification. *International Biodeterioration & Biodegradation 117*: 68-77. doi: 10.1016/j.ibiod.2016.11.022

Nazarpour, F., Abdullah, D. K., Abdullah, N. & Zamiri, A. (2013). Evaluation of biological pretreatment of rubberwood with white rot fungi for enzymatic hydrolysis. *Materials 6* (5): 2059-2073. doi: 10.3390/ma6052059

Owens, E. M., Reddy, C. A. & Grethlein, H. E. (1994). Outcome of interspecific interactions among brown-rot and white-rot wood decay fungi. *FEMS Microbiology Ecology 14* (1): 19-24. doi: 10.1111/j.1574-6941.1994.tb00086.x

Qadir, F., Shariq, M., Ahmed, A. & Sohail, M. (2018). Evaluation of a yeast co-culture for cellulase and xylanase production under solid state fermentation of sugarcane bagasse using multivariate approach. *Industrial Crops and Products 123*: 407-415. doi: 10.1016/j.indcrop.2018.07.021

Ramamurthy, V., Cheepurupalli, L., Rathore, S. S. & Ramakrishnan, J. (2017). Co-culture: A promising method in enzyme production. *International Journal of ChemTech Research 10* (6): 720-726.

Rayner, A. D. M. & Boddy, L. (1988). Fungal communities in the decay of wood. *Advances in Microbial Ecology 10*: 115-166.

Sasongko, W. T., Larasati, T. R. D., Mulyana, N. & Wahyono, T. (2019). *In vitro* gas and methane production from fermented rice straw using *Trichoderma viride* and *Phanerochaete chrysosporium* inoculant. *Materials Science and Engineering 546*: 1-7. doi: 10.1088/1757-899X/546/2/022023

Savoie, J. M., Mata, G. & Billette, C. (1998). Extracellular laccase production during hyphal interactions between *Trichoderma* sp. and shiitake, *Lentinula edodes*. *Applied Microbiology and Biotechnology 49*: 589–593. doi: 10.1007/s002530051218

Score, A. J., Palfreyman, J. W. & White, N. A. (1997). Extracellular phenoloxidase and peroxidase enzyme production during interspecific fungal interactions. *International Biodeterioration & Biodegradation 39* (2-3): 225-233. doi: 10.1016/S0964-8305(97)00012-7

Sharma, R. K. & Arora, D. S. (2013). Fungal degradation of lignocellulosic residues: An aspect of improved nutritive quality. *Critical Reviews in Microbiology 41* (1): 52-60. doi: 10.3109/1040841X.2013.791247

Silva, J. A. T. (2015). Negative results: negative perceptions limit their potential for increasing reproducibility. *Journal of Negative Results in BioMedicine 14* (12): 1-4. doi: 10.1186/s12952-015-0033-9

Singh, A. P. & Singh, T. (2014). Biotechnological applications of wood-rotting fungi: A review. *Biomass and Bioenergy 62*: 198-206. doi: 10.1016/j.biombioe.2013.12.013

Singh, P., Sulaiman, O., Hashim, R., Rupani, P. F. & Peng, L. C. (2010). Biopulping of lignocellulosic material using different fungal species: a review. *Reviews in Environmental Science and Bio/Technology 9*: 141-151. doi: 10.1007/s11157-010-9200-0

Song, Z., Vail, A., Sadowsky, M. J. & Schilling, J. S. (2012). Competition between two wood-degrading fungi with distinct influences on residues. *FEMS Microbiology Ecology 79* (1): 109-117. doi: 10.1111/j.1574-6941.2011.01201.x

Sperandio, G. B. & Filho, E. X. F. (2019). Fungal co-cultures in the lignocellulosic biorefinery context: A review. *International Biodeterioration & Biodegradation 142*: 109-123. doi: 10.1016/j.ibiod.2019.05.014

Stepanova, E. V., Koroleva, O. V., Vasilchenko, L. G., Karapetyan, K. N., Landesman, E. O., Yavmetdinov, I. S., Kozlov, Y. P. & Rabinovich, M. L. (2003). Fungal decomposition of oat straw during liquid and solid-state fermentation. *Applied Biochemistry and Microbiology 39*: 65-74. doi: 10.1023/A:1021702211169

Sundman, V. & Näse, L. (1972). The synergistic ability of some wood-degrading fungi to transform lignins and lignosulfonates on various media. *Archiv für Mikrobiologie 86*: 339-348. doi: 10.1007/bf00424990

Tao, L., Zhang, L. X., Tu, Y., Zhang, N. F., Si, B. W., Ma, T. & Diao, Q. Y. (2016). Improving the *in situ* ruminal degradability of maize stalk using fungal inoculants in dorper × thin-tailed han crossbred ewes. *Small Ruminant Research 144*: 119-125. doi: 10.1016/j.smallrumres.2016.09.001

Tsujiyama, S. & Minami, M. (2005). Production of phenol-oxidizing enzymes in the interaction between white-rot fungi. *Mycoscience 43* (4): 268-271. doi: 10.1007/S10267-005-0243-Y

Ujor, V. C., Adukwu, E. C. & Okonkwo, C. C. (2018). Fungal wars: The underlying molecular repertoires of combating mycelia. *Fungal Biology 122* (4): 191-202. doi: 10.1016/j.funbio.2018.01.001

Van Dyk, J. S. & Pletschke, B. I. (2012). A review of lignocellulose bioconversion using enzymatic hydrolysis and synergistic cooperation between enzymes - Factors affecting enzymes, conversion and synergy. *Biotechnology Advances 30* (6): 1458-1480. doi: 10.1016/j.biotechadv.2012.03.002

Van Heerden, A., Roux, N. J., Swart, J., Lubbe-Gardner, S. & Botha, A. (2008). Assessment of wood degradation by *Pycnoporus sanguineus* when co-cultured with selected fungi. *World Journal of Microbiology and Biotechnology 24* (11): 2489-2497. doi: 10.1007/s11274-008-9773-8

Vanholme, R., Demedts, B., Morreel, K., Ralph, J. & Boerjan, W. (2010). Lignin biosynthesis and structure. *Plant Physiology 153*: 895-905. doi: 10.1104/pp.110.155119

Vasil'chenko, L. G., Karapetyan, K. N., Yachkova, S. N., Zernova, E. S. & Rabinovich, M. L. (2004). Degradation of a lignin–carbohydrate substrate by soil fungi producing laccase and cellobiose dehydrogenase. *Applied Biochemistry and Microbiology 40*: 44-49. doi: 10.1023/b:abim.0000010350.17045.1c

Wang, H., Peng, L., Ding, Z., Wu, J. & Shi, G. (2015). Stimulated laccase production of *Pleurotus ferulae* JM301 fungus by *Rhodotorula mucilaginosa* yeast in co-culture. *Process Biochemistry 50* (6): 901-905. doi: 10.1016/j.procbio.2015.03.004

Wang, W., Yuan, T. & Cui, B. (2014). Biological pretreatment with white rot fungi and their co-culture to overcome lignocellulosic recalcitrance for improved enzymatic digestion. *BioResources 9* (3): 3968-3976.

White, N. A. & Boddy, L. (1992). Extracellular enzyme localization during interspecific fungal interactions. *FEMS Microbiology Letters 98* (1-3): 75-80. doi: 10.1111/j.1574-6968.1992.tb05493.x

Woodward, S. & Boddy, L. (2008). Chapter 7 - Interactions between saprotrophic fungi. *British Mycological Society Symposia Series 28*: 125-141. doi: 10.1016/S0275-0287(08)80009-4

Xie, P., Fan, L., Huang, L. & Zhang, C. (2020). An innovative co-fungal treatment to poplar bark sawdust for delignification and polyphenol enrichment. *Industrial Crops and Products 157*: 1-11. doi: 10.1016/j.indcrop.2020.112896

Yang, D., Billerbeck, G. M., Zhang, J., Rosenzweig, F. & Francois, J. (2017). Deciphering the origin, evolution, and physiological function of the subtelomeric aryl-alcohol dehydrogenase gene family in the yeast *Saccharomyces cerevisiae*. *Applied and Environmental Microbiology 84* (1): 1-16. doi: 10.1128/AEM.01553-17

Yang, R., Meng, D., Hu, X., Ni, Y. & Li, Q. (2013). Saccharification of pumpkin residues by coculturing of *Trichoderma reesei* rut-c30 and *Phanerochaete chrysosporium* burdsall with delayed inoculation timing. *Journal of Agricultural and Food Chemistry 61* (38): 9192-9199. doi: 10.1021/jf402199j

Yang, Y. S., Zhou, J. T., Lu, H., Yuan, Y. L. & Zhao, L. H. (2011). Isolation and characterization of a fungus *Aspergillus* sp. strain F-3 capable of degrading alkali lignin. *Biodegradation 22*: 1017-1027. doi: 10.1007/s10532-011-9460-6

Yao, L., Zhu, L., Xu, X., Tan, L., Sadilek, M., Fan, H., Shen, X., Yang, J., Qiao, B. & Yang, S. (2016). Discovery of novel xylosides in co-culture of basidiomycetes *Trametes versicolor* and *Ganoderma applanatum* by integrated metabolomics and bioinformatics. *Scientific Reports 6*: 332-337. doi: 10.1038/srep33237

Yavmetdinov, I. S., Stepanova, E. V., Gavrilova, V. P., Lokshin, B. V., Perminova, I. V. & Koroleva, O. V. (2003). Isolation and characterization of humin-like substances produced by wood-degrading white rot fungi. *Applied Biochemistry and Microbiology 39*: 257-264. doi: 10.1023/A:1023571426331

Zhang, J., Ke, W. & Chen, H. (2019). Enhancing laccase production by white-rot fungus *Trametes hirsuta* SSM-3 in co-culture with yeast *Sporidiobolus pararoseus* SSM-8. *Preparative Biochemistry & Biotechnology 50* (1): 1-8. doi. 10.1080/10826068.2019.1655764

Zhong, Z., Li, N., He, B., Igarashi, Y. & Luo, F. (2019). Transcriptome analysis of differential gene expression in *Dichomitus squalens* during interspecific mycelial interactions and the potential link with laccase induction. *Journal of Microbiology 57* (2): 127-137. doi: 10.1007/s12275-019-8398-y

Zhou, L. & Li, L. Y. (2016). Novel fungal consortium pretreatment of waste oat straw to enhance economical and efficient biohydrogen production. *Ecocycles 2* (2): 36-42. doi: 10.19040/ecocycles.v2i2.61