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REVIEW

Microbial utilization of lignin: available biotechnologies for its degradation and valorization

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Abstract Lignocellulosic biomasses, either from non-edible plants or from agricultural residues, stock biomacromolecules that can be processed to produce both energy and bioproducts. Therefore, they become major candidates to replace petroleum as the main source of energy. However, to shift the fossil-based economy to a bio-based one, it is imperative to develop robust biotechnologies to efficiently convert lignocellulosic streams in power and platform chemicals. Although most of the biomass processing facilities use celluloses and hemicelluloses to produce bioethanol and paper, there is no consolidated bioprocess to produce valuable compounds out of lignin at industrial scale available currently. Usually, lignin is burned to provide heat or it remains as a by-product in different streams, thus arising environmental concerns. In this way, the biorefinery concept is not extended to completion. Due to Nature offers an arsenal of biotechnological tools through microorganisms to accomplish lignin valorization or degradation, an increasing number of projects dealing with these tasks have been described recently. In this review, outstanding reports over the last 6 years are described, comprising the microbial utilization of lignin to produce a variety of valuable compounds as well as to diminish its ecological impact. Furthermore, perspectives on these topics are given.

Keywords Biocatalysis · Bioprocess · Bioremediation · Biotransformation · Lignocellulose · Lignin

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Introduction

According to recent calculations, in 15 years the global demand of energy will have increased by a 50 % (McCann and Carpita 2015). Under this scenario, it seems imperative to shift the source of both energy and chemicals from fossil carbon to renewable sources. The negative impact of the current petrol-based economy on the ecosystem pushes this need harder. Many years ago, the lignocellulosic biomass was considered as a substitute candidate to develop a bio-based economy since it offers partially oxygenated structures that could yield platform chemicals. Also, it is readily available in vast amounts—from non-edible plants and as waste of the worldwide agricultural activity—, thus satisfying productive and ecological criteria (Kawaguchi et al. 2016). However, the recalcitrant nature of this biomass—defined as the resistance of plant cell walls to deconstruction into monomeric sugars (DeMartini et al. 2013)—has been widely recognized as the main bottleneck to meet the need (Zeng et al. 2014). This characteristic mainly arises from lignin, a complex heteropolymer of interconnected phenylpropanoid units conferring mechanical strength and rigidity to plants while acting as a physical barrier to protect the cellulose and hemicellulose fractions from pathogen attack (Vanholme et al. 2010). The generation of energy, fuel, building-block chemicals, and other products out of lignocellulosic biomass is, in simple terms, referred as the biorefinery concept (Maity 2015). The production of bioethanol and paper from plant biomass only comprises the net use of the celluloses and hemicelluloses, while lignin is usually burnt to provide heat or it remains as a by product in industrial effluents, thus causing environmental damage regarding its acidic nature.

A wide range of methodologies have been developed over the years to tackle down lignin recalcitrance. Nature

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itself offers multiple opportunities to achieve lignin depolymerization through an incommensurable variety of microorganisms (Cragg et al. 2015) which, combined with chemical procedures (Li et al. 2015), could allow the development of different strategies to fulfill the biorefinery concept. Furthermore, advanced approaches have emerged to manipulate the biosynthetic plasticity of lignin in plants to ease its degradation, therefore referred as the production of designer lignins (Eudes et al. 2014).

Wood-rotting fungi are attractive biotechnological tools to harness plant biomass because of their ability to secrete a set of lignocellulolytic enzymes in vast amounts. These include species from the phyla *Ascomycota* and *Basidiomycota* such as brown-rot and white-rot fungi, respectively (Dashtban et al. 2010). From a productive perspective, mainly brown-rot fungi are used to ferment the polysaccharide fraction of plant biomass, but they exert no or little lignin degradation. On the contrary, white-rot fungi are very efficient for lignin breakdown and some of them can even exhibit high selectivity, thus leaving the cellulose and hemicellulose fractions almost intact (Makela et al. 2014). To achieve this, the latter fungi display a combination of extracellular ligninolytic enzymes, organic acids, mediators and accessory enzymes to exert their biomass-decaying activity. These enzymes comprise heme peroxidases—such as lignin, manganese, and versatile peroxidases—and laccases. A range of accessory enzymes like H_2O_2-generating oxidases are also needed (Dashtban et al. 2010). Alternatively, brown-rot fungi employ a non-enzymatic mechanism as an initial step of lignocellulose decay to produce free hydroxyl radicals through Fenton chemistry, thereby attacking lignocelluloses in a non-specific manner, enabling the penetration of the saccharification enzymes (Arantes et al. 2012).

In the last few years, some reports describing the ability of bacteria to break down lignin have emerged (Brown and Chang 2014). Due to the genetic engineering and the protein expression of fungi is often more challenging as when dealing with bacteria, the use of the latter has received great attraction (Bugg et al. 2011b). As extensively reviewed by Tian et al., most of the bacteria showing ligninolytic activities comprise the phyla *Proteobacteria*, *Actinobacteria*, *Firmicutes*, and to a lesser extent, *Cyanobacteria*, *Bacteriodetes* and *Spirochaetes* (Tian et al. 2014).

This review deals with the microbial utilization of lignin from two main focuses: (1) the solely degradative approaches—describing the polymer breakdown for the ease of pulping, the bioremediation of lignin-affected environments, or the preparation of animal feed with low lignin content, and (2) the lignin harnessing strategies leading to a range of per se valuable chemicals, even further transformable to an array of bio-based compounds of industrial interest.

Lignin depolymerization bioprocesses

Considering the aromatic nature of lignin, the key step for its complete degradation is to overcome the resonance energy that stabilizes the ring structures (Fuchs et al. 2011). As stated above, lignin breakdown is achieved mostly by aerobic fungi and some bacteria. As follows, recent reports describing the microbial degradation of lignin with a variety of purposes are described. It is known that a few archaea exhibit ligninolytic activity in an aerobic fashion (Fuchs et al. 2011). However, this is not covered in this review.

Isolation and utilization of fungi for lignin breakdown

The ultimate roles of fungi in the production of ethanol from lignocellulosic biomass—enabling the access to fermentable sugars- as well as in the papermaking process—particularly in the bleaching step—have been widely described by several authors over the last years (Lomascolo et al. 2011; Paliwal et al. 2012). Furthermore, a variety of processes comprising the use of fungi to reduce the lignin content in different environments (Kulikova et al. 2011) or to improve ruminant feedstock nutritive quality (Sharma and Arora 2015; van Kuijk et al. 2015) is readily available from the literature.

Arimoto et al. (2015) performed the molecular breeding of *Gloeophyllum trabeum* KU-41 by the overexpression of an endogenous laccase producing a 45 % increase in the ethanol yield (0.25 g/L in 12 days) from Japanese cedar wood in comparison with the wild-type strain as a consequence of an enhanced lignin degradation. Chang et al. (2012) found a *Fusarium moniliforme* strain with high delignification power on rice straw but almost inactive on the holocellulose fraction, showing enough selectivity to represent a good choice to prepare ruminant feedstock. Furthermore, Knežević et al. (2016) determined the addition of *p*-anisidine can significantly shift the selectivity of the white-rot fungi *Trametes hirsuta* towards lignin (up to 1.1 g/L in 19 days) when cultured under the presence of lignocellulosic biomasses such as wheat and bran straw. Ryazanova et al. (2015) studied the oxidative degradation of lignin by *Trichoderma asperellum* MG-97/6, demonstrating the occurrence of (1) demethoxylation and subsequent hydroxylation reactions as initial steps, (2) the disruption of the Cα-Cβ bonds and the oxidation of primary hydroxyls to carboxyl groups, and (3) the disruption of the aromatic rings. Liang et al. (2010) determined the addition of small amounts of a dirhamnolipid biosurfactant increased the ligninolytic activity (ca. 5.2 g/L in 32 days) of the white-rot fungus *Phanerochaete chrysosporium* on rice straw. On the other hand, Arun and Eyini identified—

among 130 wild basidiomycetes—a strain of *Phellinus* capable of degrading lignin with the concomitant production of a biosurfactant (1.8 and 3.4 g/L, respectively, in 10 days) (Arun and Eyini 2011). Moreover, Hainal et al. (2012) studied the impact of the addition of lignin from wheat straw in cultures of *Rhodotorula* sp. and found it not only had a positive effect on the microbial biomass yield as desired but also triggered the biosynthesis of carotenoids. Using post-industrial lignin as substrate, Korniłłowicz-Kowalska and Rybczyńska (2015) detected 610 fungal strains exhibiting ligninolytic activity in lignin-rich environments, most of them belonging to the *Aspergillus*, *Fusarium*, *Gliocladium* and *Trichoderma* genera. In particular, the strains of *Aspergillus* sp. LII11 and *Fusarium solani* BS11 were among the best degraders, consuming 0.05 and 0.07 g/L of lignin in 14 days, respectively. These reports are summarized in Table 1.

Discovery and application of new bacterial lignin degraders

Several reports have recently emerged describing the isolation of bacteria from lignin-rich environments and its use to degrade this polymer with different purposes, most of them aiming to decrease the lignin content in pulping streams. Chen et al. (2012) cultured *Comamonas* sp. from fluids of bamboo eroded slips capable of growing on several lignin-derived compounds and degrading up to 0.9 g/L Kraft lignin after 7 days. The same group also designed an efficient bioaugmentation strategy to treat black liquor streams using the mentioned *Comamonas* sp. strain in combination with *Pandoraea* B-6 and *Aspergillus* F-1 strains, reporting a lignin removal of 78 g/L after 9 days (Zheng et al. 2013). Paliwal et al. (2015) isolated two indigenous bacterial strains, *Bacillus megaterium* ETLB-1 and *Pseudomonas plecoglossicida* ETLB-3, from soil contaminated with paper mill effluent and reported they were capable of reducing the lignin content in black liquor up to 0.8 g/L in 7 days when co-immobilized in corncob cubes. Elsalam and Bohobail (2016) reported the capability of two thermophilic bacteria isolated from soil, water and pulp paper sludge, namely *Bacillus subtilis* and *B. licheniformis*, to biodegrade 0.7 and 0.6 g/L of Kraft lignin in 7 days, respectively. Lv et al. (2014) set a microbial consortium showing up to 0.2 g/L of lignin degradation in 7 days when supplemented with 0.5 g/L of ammonium chloride and 2 g/L of sucrose. Mathews et al. (2016) compared two *Paenibacillus glucanolyticus* strains, the type one and another isolated from pulp mill waste, and found that both were capable of degrading a range of lignin-derived chemicals regardless oxygenation. Interestingly, they demonstrated that although both strains were able to break down lignin under anaerobic conditions, only the adapted *P. glucoanolyticus* strain exhibited lignin degradation activity in aired cultures.

Ligninolytic microorganisms are excellent biotechnological tools for the ease of pulping. Apart from the widely used white-rot fungi, lignin-degrading bacteria are also becoming studied and applied in biopulping processes. Wang et al. prepared a bacterial consortium out of

Table 1 Lignin breakdown bioprocesses involving fungi

Lignin source	Fungi	Degradation capacity (g/L)	Time (days)	Application	Reference
Dioxane lignin	*Trichoderma asperellum* MG-97/6	NS	NS	Pulp bleaching, bioethanol production	Ryazanova et al. (2015)
Japanese cedar wood	*Gloeophyllum trabeum* KU-41	NS	12	Bioethanol production	Arimoto et al. (2015)
NS	*Phelinus* sp.	1.8	10	Bioremediation, biosufactant production	Arun and Eyini (2011)
Post-industrial lignin	*Aspergillus* sp. LII11	0.05	14	Bioremediation	Korniłłowicz-Kowalska and Rybczyńska (2015)
	Fusarium solani BS11	0.07	14		
Rice straw	*Phanerochate chrysosporium*	5.2	32	Bioremediation	Liang et al. (2010)
Rice straw	*Fusarium moniliforme*	NS	NS	Ruminant feedstock preparation	Chang et al. (2012)
Wheat and bran straw	*Trametes hirsuta*	1.1	19	NS	Kneževic et al. (2016)
Wheat straw	*Rhodotorula* spp.	5	4	Microbial biomass and carotenoid production	Hainal et al. (2012)

NS not specified

sludge from reeds ponds with the capability of breaking down 0.6 g/L of lignin in 15 days at 30 °C in a static culture. Around the 80 % of the bacterial diversity was identified and assigned to 10 different genera. Furthermore, the authors used this consortium to conduct a biological pretreatment for pulping, achieving better physical characteristics of pulp while lowering the energy consumption when compared with the chemical pretreatment, albeit shorter process time would be desired (Wang et al. 2013).

Characterized by high biomass decay, forest and agricultural soils often offer a plethora of readily available lignocellulolytic microorganisms. Yang et al. (2012) found two *Streptomyces* species cultured from forest soil exhibiting up to 1.1 g/L of alkali lignin in 12 days when co-cultured with the white-rot fungi *Pleurotus ostreatus*, and qualitative identified a range of lignin decomposition products. Harith et al. (2014) isolated three bacterial strains from decayed plants, identified as *Klebsiella* sp., *Enterobacter* sp. and *Bacillus cereus*, and qualitatively determined their ligninolytic potential. Akita et al. (2016) cultured from leaf soil a bacteria identified as *Burkholderia* sp. and assessed its degradation activity on alkali lignin qualitatively. Taylor et al. (2012) detected 12 bacterial strains able to depolymerize Kraft lignin from woodland soil incubated in enrichment cultures containing wheat straw lignocellulose by employing a practical assay developed by their own group comprising nitrated lignin (Ahmad et al. 2010). Two of these isolates—namely *Microbacterium* A1.1 and *Sphingobacterium* T2-when cultured with wheat straw lignocellulose also produced oxalic acid and protocatechuic acid, valuable chemicals which could come from the oxidative C–C cleavage of the β-aryl ether moiety in lignin triggered by these microbes. Bandounas et al. (2011) isolated bacteria from soil collected from beneath decomposing wood logs by enrichment on Kraft lignin and found two strains identified as *Pandoraea norimbergensis* LD001 and *Pseudomonas* sp. LD002 that grew on high and low-molecular weight lignin.

In the last years, the study of the gastrointestinal microbiota from lignocellulose-feeding species has gained attraction (Yue et al. 2013). Fang et al. (2012) performed a phylogenetic analysis of a giant panda fecal microbiome, thereby identifying phylotypes affiliated with lignin-degrading bacteria like *Pseudomonas putida* and those from mangrove forest. Recently, Suman et al. used guaiacylglycerol-β-guaiacylether as a lignin model substrate to screen for degraders in the termite gut. A *Trabulsiella* sp. showed 0.1 g/L as maximal ligninolytic activity after 14 days (Suman et al. 2016). The bacterial lignin degradation processes described above are summarized in Table 2.

Microbial lignin upgrading strategies

As stated above, for the biorefinery concept to be economically feasible, the utilization of the entire cell wall of the lignocellulosic biomass is mandatory. Hence, lignin must not be discarded but used to prepare valuable chemicals. In recent, comprehensive manuscripts, Bugg and Beckham reviewed the microbial pathways for lignin breakdown, comprising the (1) β-aryl ether, (2) biphenyl, (3) diarylpropane, (4) phenylcoumarane and pinoresinol, (5) ferulic acid, and (6) protocatechuic acid oxidative cleavage routes (Bugg et al. 2011a, b; Beckham et al. 2016). A number of fascinating works to produce valuable and renewable compounds out of lignin through these pathways have been reported in recent years, and they are described as follows.

Kosa and Ragauskas pioneered the production of neutral lipids from lignin model compounds using oleaginous bacteria. The authors not only described the synthesis of triacylglycerols out of *p*-hydroxybenzoic acid and vanillic acid using *Rhodococcus opacus* DSM 1069 as biocatalyst—presumably utilizing the β-ketoadipate pathway—, but also prepared their methyl esters and determined they were suitable for biodiesel applications (Kosa and Ragauskas 2012). In a further work, these authors studied the use of ethanol organosolv lignin and an ultrasonicated sample of it as substrates of *R. opacus* DSM 1069 with lipid production purposes and found these were poor substrates in comparison with the lignin model compounds (Kosa and Ragauskas 2013). Although the microbial catalyst is a powerful aromatic oligomer and monomer degrader, unfortunately it exhibits poor ligninolytic activity. Thus, these results suggest a (bio)chemical lignin oxidation step should be conducted before the lipid production bioprocess. In effect, in a subsequent report, Wei et al. (2015) included an alkali-oxygen pretreatment of Kraft lignin to allow *R. opacus* DSM 1069 to take up the substrate to produce up to 0.07 g/L of lipids in 36 h. Interestingly, an oxidative biological alternative was recently studied by Zhao et al. (2016) who showed the combination of *R. opacus* DSM 44,193 strain and laccase from *Trametes versicolor* in batch was synergistic enough so as to effectively promote a lipid accumulation of 0.14 g/L in 6 days directly from Kraft lignin.

To contribute with the necessity to find efficient microorganisms to produce valuable chemicals out of lignin, Salvachua and coworkers screened 14 bacteria species to assess their ligninolytic activity, aromatic uptake capability, and polyhydroxyalkanoate- and fatty acid-producing profiles. They worked both under nitrogen-limiting and nutrient-rich conditions, using alkaline pretreated liquor as a lignin-enriched biorefinery stream model. Among them,

Table 2 Procedures comprising lignin degradation by bacteria

Lignin source	Bacteria	Degradation capacity (g/L)	Time (days)	Application	Reference
Alkali lignin	*Streptomyces* spp.[c]	1.1	12	Bioremediation	Yang et al. (2012)
Alkali lignin	*Klebsiella* sp., *Enterobacter* sp., *Bacillus cereus*	NS	NS	Bioremediation, bioethanol production	Harith et al. (2014)
Alkali lignin	*Burkholderia* sp.	NS	NS	Bioremediation	Akita et al. (2016)
Black liquor	*Comamonas* sp.[a]	78	9	Bioremediation	Zheng et al. (2013)
Black liquor	*Bacillus megaterium* ETLB-1, *Pseudomonas plecoglossicida* ETLB-3	0.8	7	Bioremediation	Paliwal et al. (2015)
Commercial	*Bacillus* sp., *Pseudomonas putida*[b]	0.2	7	Bioremediation	Lv et al. (2014)
Commercial	*Paenibacillus glucanolyticus*	NS	NS	Bioremediation	Mathews et al. (2016)
Commercial	Consortium	0.6	15	Pulping	Wang et al. (2013)
Guaiacylglycerol-β-guaiacylether	*Trabulsiella* sp.	0.1	14	Bio-based chemical production	Suman et al. (2016)
Kraft lignin	*Comamonas* sp.	0.9	7	Bioremediation	Chen et al. (2012)
Kraft lignin	*Bacillus subtilis*	0.7	7	Bioremediation	Elsalam and Bahobail (2016)
	Bacillus licheniformis	0.6	7	Bioremediation	
Kraft lignin	*Microbacterium* A1.1, *Sphingobacterium* T2 and 10 other strains	NS	NS	Bio-based chemical production	Taylor et al. (2012)
Kraft lignin	*Pandoraea norimbergensis* LD001, *Pseudomonas* sp. LD002	NS	NS	Bio-based chemical production	Bandounas et al. (2011)

NS not specified

[a] The strains *Pandoraea* B-6 and *Aspergillus* F-1 were used in combination with *Comamonas* sp

[b] Also, two microorganisms obtained through inter-kingdom protoplast fusion technology with fungi and bacteria were used

[c] This strain was co-cultured with the white-rot fungi *Pleurotus ostreatus*

the authors identified *Pseudomonas putida* KT2440, *P. putida* mt-2, *Amycolatopsis* sp. 75iv2, *Acinetobacter* sp. ADP1, *Cupriavidus necator* H16, and *Rhodococcus jostii* RHA1 as the most effective strains, thus becoming prominent candidates for further optimization (Salvachua et al. 2015).

Triggered by the release of its genome sequence, *R. jostii* RHA1 (McLeod et al. 2006) has served as an attractive engineering platform to funnel lignin-derived chemicals towards a desired product. Extraordinarily, Mycroft et al. engineered *R. jostii* RHA1 to re-route the metabolic fate of the lignin depolymerization product protocatechuic acid to produce pyridine-2,4-dicarboxylic acid (PDCA). The biocatalyst yielded 0.12 g/L of PDCA after 9 days when grown in a minimal media containing 10 g/L of wheat straw lignocellulose, or 0.05 g/L of the same product in 4 days when cultured in the presence of 5 g/L of Kraft lignin. Noticeably, PDCA could serve as a raw material for bioplastic synthesis (Mycroft et al. 2015). On the other hand, Sainsbury et al. (2013) altered the lignin breakdown pathway in *R. jostii* RHA1 to bioaccumulate up to 0.1 g/L of vanillin—a chemical of paramount importance for the flavor and food industries—after 6 days when grown in a minimal media including 25 g/L of wheat straw lignocellulose.

Both the chemical and the biological oxidative degradations of lignin release a range of low molecular weight compounds which may be employed as platform renewable chemicals. In a recent report, our group described the preparation of different products from vanillic acid, veratric acid—two lignin oxidative depolymerization products-and other related benzoic acids in a structure-dependent fashion using a wild-type fungus, *Aspergillus flavus.* When using vanillic acid as substrate, the biocatalyst exhibited exquisite selectivity towards the oxidative decarboxylation product, 2-methoxybenzene-1,4-diol. Interestingly, when assaying a set of structurally related substrates, *A. flavus* displayed the oxidative removal of the carboxyl moiety or its reduction to the primary alcohol whether electron withdrawing or donating groups were present in the aromatic ring, respectively. Additionally, the fungal catalyst proved to be tolerant to high concentrations of vanillic acid (up to 8 g/L) (Palazzolo et al. 2015), thus demonstrating its potential application in the preparation of an array of renewable compounds used as starting chemicals for polymer chemistry (Fache et al. 2014; Upton and Kasko

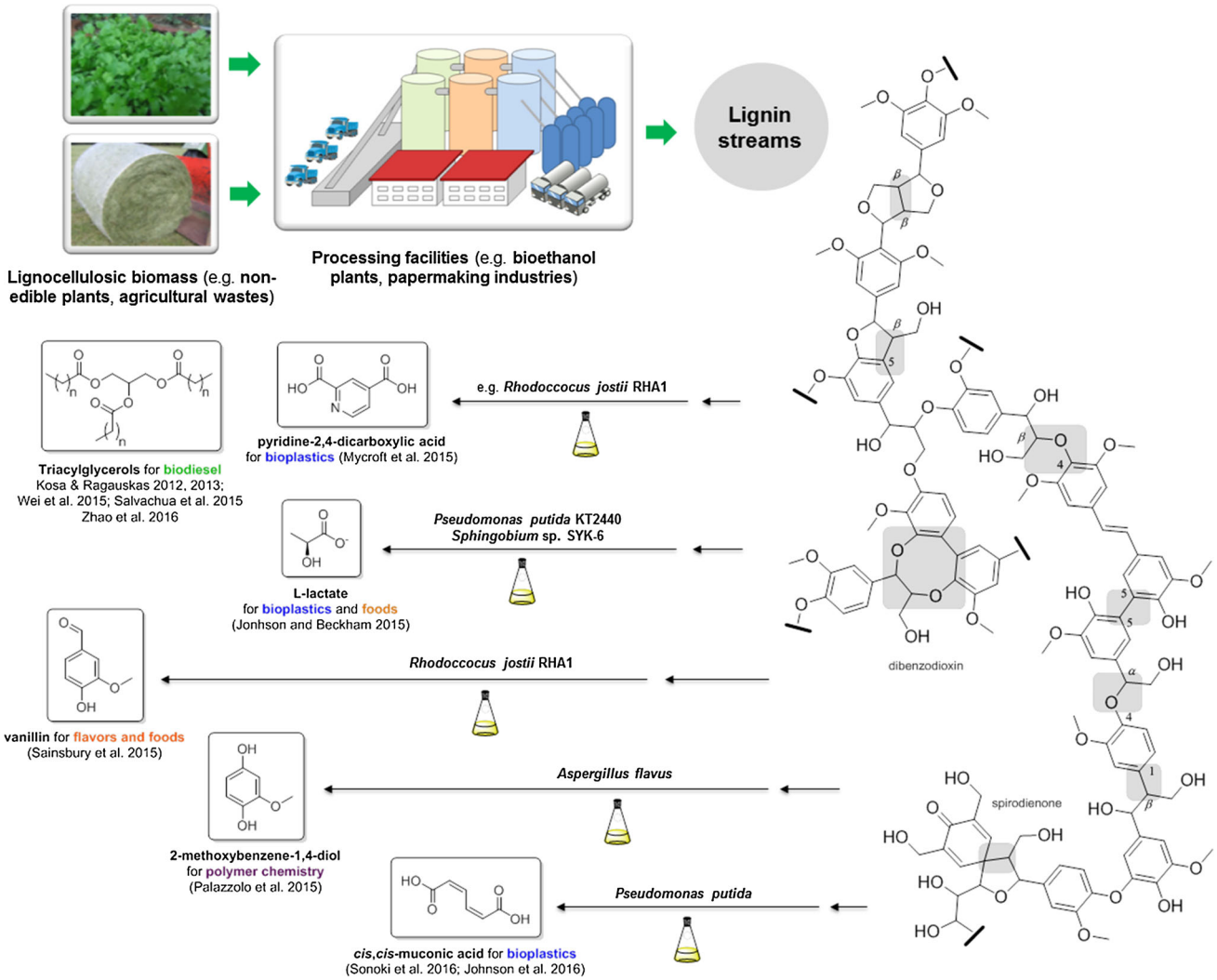

Fig. 1 Currently available lignin valorization strategies

2016). In an early work, Davis and Sello suggested the β-ketoadipate pathway—the major utilization route for lignin-derived aromatic compounds in microorganisms—in *Streptomyces* bacteria could be engineered for the biotechnological upgrade of lignin and its aromatic monomers (Davis and Sello 2010). Then, Johnson and Beckham (2015) remarkably showed the ring-cleavage pathways of lignin aromatic monomers in aerobic microorganisms can be interchanged with one another, thereby affecting the balance of acetyl-CoA, succinate, pyruvate, reducing equivalents regenerated and CO_2 emitted before entering to the TCA cycle. As shown by the authors, the replacement of the endogenous protocatechuate *ortho* pathway of *Pseudomonas putida* KT2440 with a *meta*-cleavage one from *Sphingobium* sp. SYK-6 resulted in an almost five-fold increase in pyruvate production from benzoate, which in turn could be biotransformed to L-lactate with 41 % (*w*/*w*) yield. These findings are of special interest to develop strategies to convert lignin-derived aromatic compounds into valuable chemicals.

Bio-based *cis*,*cis*-muconic acid is believed to have an incommensurable market value since it can be easily converted to adipic acid, a platform chemical employed to synthetize a variety of plastics like nylon, polyurethanes and polyethylene terephthalate (Curran et al. 2013). The biotechnological production of this compound typically involves benzoic acid—either from biomass or petroleum-based sources—as the starting material to enter the so-called β-ketoadipate pathway. As shown by Sonoki et al. (2014) a recent trend suggest it can be produced out of vanillin albeit with some obstacles, like the decarboxylation of protocatechuate to catechol. To circumvent this bottleneck, Johnson et al. have very recently engineered a *Pseudomonas putida* strain by co-expressing its protocatechuate decarboxylase with two metabolically associated proteins, thereby enhancing the activity of the key enzyme.

This recombinant biocatalyst was capable to produce more than 15 g/L of *cis*,*cis*-muconic acid from the lignin monomer *p*-coumaric acid (Johnson et al. 2016).

The above-described bioprocesses dealing with lignin upgrading are schematically represented in Fig. 1.

Future considerations

As rigorously described, there are multiple biotechnological options for the utilization of lignin available currently. Nevertheless, for these bench procedures to be adopted by the industry, economic feasibility must be evaluated and guaranteed. With this regard—and with the aid of molecular biology and metabolic engineering—cost-effective bioprocesses should be design. Both traditional and advanced screening techniques are still needed, considering an immeasurable portion of the earth microbiome remains uncultured (Gilbert et al. 2014). Moreover, the already-known ligninolytic microorganisms have not been fully studied yet (Dashtban et al. 2010). Therefore, reports emerging from environmental metagenomics (Armstrong et al. 2015; Strachan et al. 2014) as well as from next generation sequencing technologies (Kameshwar and Qin 2016), would be of paramount help. Furthermore, the designer lignin concept may be further developed so as to ease the lignin breakdown and valorization in practice (Mottiar et al. 2016).

The lignin utilization strategies are, as shown, far to be ineffective nor just a few. For these reasons, we believe it is time to leave behind the saying "you can make anything from lignin but money". Instead, we encourage scientists and industrials to deeply survey the literature reports presented here and the ones coming, and to conceive productive scenarios to harness lignin.

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Compliance with ethical standards

Conflict of interest The authors declare no commercial or financial conflict of interest.

References

Ahmad M, Taylor CR, Pink D, Burton K, Eastwood D, Bending GD, Bugg TD (2010) Development of novel assays for lignin degradation: comparative analysis of bacterial and fungal lignin degraders. Mol BioSyst 6:815–821. doi:10.1039/b908966g

Akita H, Kimura Z-I, Yusoff MZM, Nakashima N, Hoshino T (2016) Isolation and characterization of *Burkholderia* sp. strain CCA53 exhibiting ligninolytic potential. Springerplus 5:596. doi:10.1186/s40064-016-2237-y

Arantes V, Jellison J, Goodell B (2012) Peculiarities of brown-rot fungi and biochemical Fenton reaction with regard to their potential as a model for bioprocessing biomass. Appl Microbiol Biotechnol 94:323–338. doi:10.1007/s00253-012-3954-y

Arimoto M et al (2015) Molecular breeding of lignin-degrading brown-rot fungus *Gloeophyllum trabeum* by homologous expression of laccase gene. AMB Express 5:81. doi:10.1186/s13568-015-0173-9

Armstrong Z, Mewis K, Strachan C, Hallam SJ (2015) Biocatalysts for biomass deconstruction from environmental genomics. Curr Opin Chem Biol 29:18–25. doi:10.1016/j.cbpa.2015.06.032

Arun A, Eyini M (2011) Comparative studies on lignin and polycyclic aromatic hydrocarbons degradation by basidiomycetes fungi. Bioresour Technol 102:8063–8070. doi:10.1016/j.biortech.2011.05.077

Bandounas L, Wierckx NJ, de Winde JH, Ruijssenaars HJ (2011) Isolation and characterization of novel bacterial strains exhibiting ligninolytic potential. BMC Biotechnol 11:94. doi:10.1186/1472-6750-11-94

Beckham GT, Johnson CW, Karp EM, Salvachúa D, Vardon DR (2016) Opportunities and challenges in biological lignin valorization. Curr Opin Biotechnol 42:40–53. doi:10.1016/j.copbio.2016.02.030

Brown ME, Chang MC (2014) Exploring bacterial lignin degradation. Curr Opin Chem Biol 19:1–7. doi:10.1016/j.cbpa.2013.11.015

Bugg TD, Ahmad M, Hardiman EM, Rahmanpour R (2011a) Pathways for degradation of lignin in bacteria and fungi. Nat Product Rep 28:1883–1896. doi:10.1039/c1np00042j

Bugg TD, Ahmad M, Hardiman EM, Singh R (2011b) The emerging role for bacteria in lignin degradation and bio-product formation. Curr Opin Biotechnol 22:394–400. doi:10.1016/j.copbio.2010.10.009

Chang AJ, Fan J, Wen X (2012) Screening of fungi capable of highly selective degradation of lignin in rice straw. Int Biodeterior Biodegradation 72:26–30. doi:10.1016/j.ibiod.2012.04.013

Chen YH, Chai LY, Zhu YH, Yang ZH, Zheng Y, Zhang H (2012) Biodegradation of kraft lignin by a bacterial strain *Comamonas* sp. B-9 isolated from eroded bamboo slips. J Appl Microbiol 112:900–906. doi:10.1111/j.1365-2672.2012.05275.x

Cragg SM et al (2015) Lignocellulose degradation mechanisms across the tree of life. Curr Opin Chem Biol 29:108–119. doi:10.1016/j.cbpa.2015.10.018

Curran KA, Leavitt JM, Karim AS, Alper HS (2013) Metabolic engineering of muconic acid production in *Saccharomyces cerevisiae*. Metab Eng 15:55–66. doi:10.1016/j.ymben.2012.10.003

Dashtban M, Schraft H, Syed TA, Qin W (2010) Fungal biodegradation and enzymatic modification of lignin. Int J Biochem Mol Biol 1:36–50

Davis JR, Sello JK (2010) Regulation of genes in *Streptomyces* bacteria required for catabolism of lignin-derived aromatic compounds. Appl Microbiol Biotechnol 86:921–929. doi:10.1007/s00253-009-2358-0

DeMartini JD, Pattathil S, Miller JS, Li H, Hahn MG, Wyman CE (2013) Investigating plant cell wall components that affect biomass recalcitrance in poplar and switchgrass. Energy Environ Sci 6:898–909. doi:10.1039/C3EE23801F

Elsalam HE, Bahobail AS (2016) Lignin biodegradation by thermophilic bacterial isolates from Saudi Arabia research journal of pharmaceutical. Biol Chem Sci 7:1413–1424

Eudes A, Liang Y, Mitra P, Loqué D (2014) Lignin bioengineering. Curr Opin Biotechnol 26:189–198. doi:10.1016/j.copbio.2014.01.002

Fache M, Darroman E, Besse V, Auvergne R, Caillol S, Boutevin B (2014) Vanillin, a promising biobased building-block for monomer synthesis. Green Chem 16:1987–1998. doi:10.1039/C3GC42613K

Fang W et al (2012) Evidence for lignin oxidation by the giant panda fecal microbiome. PLoS ONE 7:e50312. doi:10.1371/journal.pone.0050312

Fuchs G, Boll M, Heider J (2011) Microbial degradation of aromatic compounds—from one strategy to four. Nat Rev Microbiol 9:803–816. doi:10.1038/nrmicro2652

Gilbert JA, Jansson JK, Knight R (2014) The Earth Microbiome project: successes and aspirations. BMC Biol 12:1–4. doi:10.1186/s12915-014-0069-1

Hainal A, Capraru A, Volf I, Popa V (2012) Lignin as a carbon source for the cultivation of some *Rhodotorula* species. Cellul Chem Technol 46:87–96

Harith Z, Ibrahim NA, Yusoff N (2014) Isolation and identification of locally isolated lignin degrading bacteria. J Sustain Sci Manag 9:114–118

Johnson CW, Beckham GT (2015) Aromatic catabolic pathway selection for optimal production of pyruvate and lactate from lignin. Metab Eng 28:240–247. doi:10.1016/j.ymben.2015.01.005

Johnson CW, Salvachúa D, Khanna P, Smith H, Peterson DJ, Beckham GT (2016) Enhancing muconic acid production from glucose and lignin-derived aromatic compounds via increased protocatechuate decarboxylase activity. Metab Eng Commun 3:111–119. doi:10.1016/j.meteno.2016.04.002

Kameshwar AK, Qin W (2016) Recent developments in using advanced sequencing technologies for the genomic studies of lignin and cellulose degrading microorganisms. Int J Biol Sci 12:156–171. doi:10.7150/ijbs.13537

Kawaguchi H, Hasunuma T, Ogino C, Kondo A (2016) Bioprocessing of bio-based chemicals produced from lignocellulosic feedstocks. Curr Opin Biotechnol 42:30–39. doi:10.1016/j.copbio.2016.02.031

Knežević A, Stajić M, Jovanović VM, Kovačević V, Ćilerdžić J, Milovanović I, Vukojević J (2016) Induction of wheat straw delignification by *Trametes* species Scientific Reports 6:26529 doi:10.1038/srep26529 http://www.nature.com/articles/srep26529#supplementary-information

Korniłłowicz-Kowalska T, Rybczyńska K (2015) Screening of microscopic fungi and their enzyme activities for decolorization and biotransformation of some aromatic compounds. Int J Environ Sci Technol 12:2673–2686. doi:10.1007/s13762-014-0656-2

Kosa M, Ragauskas AJ (2012) Bioconversion of lignin model compounds with oleaginous Rhodococci. Appl Microbiol Biotechnol 93:891–900. doi:10.1007/s00253-011-3743-z

Kosa M, Ragauskas AJ (2013) Lignin to lipid bioconversion by oleaginous Rhodococci. Green Chem 15:2070–2074. doi:10.1039/C3GC40434J

Kulikova HA, Kliain OI, Stepanova EV, Koroleva OV (2011) Use of basidiomycetes in industrial waste processing and utilization technologies: fundamental and applied aspects (review). Prikl Biokhim Mikrobiol 47:619–634

Li C, Zhao X, Wang A, Huber GW, Zhang T (2015) Catalytic transformation of lignin for the production of chemicals and fuels. Chem Rev 115:11559–11624. doi:10.1021/acs.chemrev.5b00155

Liang YS et al (2010) Biodelignification of rice straw by *Phanerochaete chrysosporium* in the presence of dirhamnolipid. Biodegradation 21:615–624. doi:10.1007/s10532-010-9329-0

Lomascolo A, Uzan-Boukhris E, Herpoel-Gimbert I, Sigoillot JC, Lesage-Meessen L (2011) Peculiarities of *Pycnoporus species* for applications in biotechnology. Appl Microbiol Biotechnol 92:1129–1149. doi:10.1007/s00253-011-3596-5

Lv Y, Chen Y, Sun S, Hu Y (2014) Interaction among multiple microorganisms and effects of nitrogen and carbon supplementations on lignin degradation. Bioresour Technol 155:144–151. doi:10.1016/j.biortech.2013.12.012

Maity SK (2015) Opportunities, recent trends and challenges of integrated biorefinery: part II. Renew Sustain Energy Rev 43:1446–1466. doi:10.1016/j.rser.2014.08.075

Makela MR, Donofrio N, de Vries RP (2014) Plant biomass degradation by fungi. Fungal Genet Biol 72:2–9. doi:10.1016/j.fgb.2014.08.010

Mathews SL, Grunden AM, Pawlak J (2016) Degradation of lignocellulose and lignin by *Paenibacillus glucanolyticus*. Int Biodeterior Biodegradation 110:79–86. doi:10.1016/j.ibiod.2016.02.012

McCann MC, Carpita NC (2015) Biomass recalcitrance: a multi-scale, multi-factor, and conversion-specific property. J Exp Bot 66:4109–4118. doi:10.1093/jxb/erv267

McLeod MP et al (2006) The complete genome of *Rhodococcus* sp. RHA1 provides insights into a catabolic powerhouse. Proc Natl Acad Sci USA 103:15582–15587. doi:10.1073/pnas.0607048103

Mottiar Y, Vanholme R, Boerjan W, Ralph J, Mansfield SD (2016) Designer lignins: harnessing the plasticity of lignification. Curr Opin Biotechnol 37:190–200. doi:10.1016/j.copbio.2015.10.009

Mycroft Z, Gomis M, Mines P, Law P, Bugg TDH (2015) Biocatalytic conversion of lignin to aromatic dicarboxylic acids in *Rhodococcus jostii* RHA1 by re-routing aromatic degradation pathways. Green Chem 17:4974–4979. doi:10.1039/C5GC01347J

Palazzolo MA, Mascotti ML, Lewkowicz ES, Kurina-Sanz M (2015) Self-sufficient redox biotransformation of lignin-related benzoic acids with *Aspergillus flavus*. J Ind Microbiol Biotechnol 42:1581–1589. doi:10.1007/s10295-015-1696-4

Paliwal R, Rawat AP, Rawat M, Rai JP (2012) Bioligninolysis: recent updates for biotechnological solution. Appl Biochem Biotechnol 167:1865–1889. doi:10.1007/s12010-012-9735-3

Paliwal R, Uniyal S, Rai JP (2015) Evaluating the potential of immobilized bacterial consortium for black liquor biodegradation. Environ Sci Pollut Res Int 22:6842–6853. doi:10.1007/s11356-014-3872-x

Ryazanova TV, Chuprova NA, Luneva TA (2015) Effect of trichoderma fungi on lignin from tree species barks. Catal Ind 7:82–89. doi:10.1134/s2070050415010134

Sainsbury PD, Hardiman EM, Ahmad M, Otani H, Seghezzi N, Eltis LD, Bugg TDH (2013) Breaking down lignin to high-value chemicals: the conversion of lignocellulose to vanillin in a gene deletion mutant of *Rhodococcus jostii* RHA1. ACS Chem Biol 8:2151–2156. doi:10.1021/cb400505a

Salvachua D, Karp EM, Nimlos CT, Vardon DR, Beckham GT (2015) Towards lignin consolidated bioprocessing: simultaneous lignin depolymerization and product generation by bacteria. Green Chem 17:4951–4967. doi:10.1039/C5GC01165E

Sharma RK, Arora DS (2015) Fungal degradation of lignocellulosic residues: an aspect of improved nutritive quality. Crit Rev Microbiol 41:52–60. doi:10.3109/1040841x.2013.791247

Sonoki T, Morooka M, Sakamoto K, Otsuka Y, Nakamura M, Jellison J, Goodell B (2014) Enhancement of protocatechuate decarboxylase activity for the effective production of muconate from lignin-related aromatic compounds. J Biotechnol 192(Pt A):71–77. doi:10.1016/j.jbiotec.2014.10.027

Strachan CR et al (2014) Metagenomic scaffolds enable combinatorial lignin transformation. Proc Natl Acad Sci USA 111:10143–10148. doi:10.1073/pnas.1401631111

Suman SK, Dhawaria M, Tripathi D, Raturi V, Adhikari DK, Kanaujia PK (2016) Investigation of lignin biodegradation by *Trabulsiella* sp. isolated from termite gut. Int Biodeterior Biodegradation 112:12–17. doi:10.1016/j.ibiod.2016.04.036

Taylor CR, Hardiman EM, Ahmad M, Sainsbury PD, Norris PR, Bugg TD (2012) Isolation of bacterial strains able to metabolize lignin from screening of environmental samples. J Appl Microbiol 113:521–530. doi:10.1111/j.1365-2672.2012.05352.x

Tian JH, Pourcher AM, Bouchez T, Gelhaye E, Peu P (2014) Occurrence of lignin degradation genotypes and phenotypes among prokaryotes. Appl Microbiol Biotechnol 98:9527–9544. doi:10.1007/s00253-014-6142-4

Upton BM, Kasko AM (2016) Strategies for the conversion of lignin to high-value polymeric materials: review and perspective. Chem Rev 116:2275–2306. doi:10.1021/acs.chemrev.5b00345

van Kuijk SJ, Sonnenberg AS, Baars JJ, Hendriks WH, Cone JW (2015) Fungal treated lignocellulosic biomass as ruminant feed ingredient: a review. Biotechnol Adv 33:191–202. doi:10.1016/j.biotechadv.2014.10.014

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

Wang Y, Liu Q, Yan L, Gao Y, Wang Y, Wang W (2013) A novel lignin degradation bacterial consortium for efficient pulping. Bioresour Technol 139:113–119. doi:10.1016/j.biortech.2013.04.033

Wei Z, Zeng G, Huang F, Kosa M, Huang D, Ragauskas AJ (2015) Bioconversion of oxygen-pretreated Kraft lignin to microbial lipid with oleaginous *Rhodococcus opacus* DSM 1069. Green Chem 17:2784–2789. doi:10.1039/C5GC00422E

Yang YS, Zhou JT, Lu H, Yuan YL, Zhao LH (2012) Isolation and characterization of *Streptomyces* spp. strains F-6 and F-7 capable of decomposing alkali lignin. Environ Technol 33:2603–2609. doi:10.1080/09593330.2012.672473

Yue ZB, Li WW, Yu HQ (2013) Application of rumen microorganisms for anaerobic bioconversion of lignocellulosic biomass. Bioresour Technol 128:738–744. doi:10.1016/j.biortech.2012.11.073

Zeng Y, Zhao S, Yang S, Ding SY (2014) Lignin plays a negative role in the biochemical process for producing lignocellulosic biofuels. Curr Opin Biotechnol 27:38–45. doi:10.1016/j.copbio.2013.09.008

Zhao C, Xie S, Pu Y, Zhang R, Huang F, Ragauskas AJ, Yuan JS (2016) Synergistic enzymatic and microbial lignin conversion. Green Chem 18:1306–1312. doi:10.1039/C5GC01955A

Zheng Y, Chai LY, Yang ZH, Tang CJ, Chen YH, Shi Y (2013) Enhanced remediation of black liquor by activated sludge bioaugmented with a novel exogenous microorganism culture. Appl Microbiol Biotechnol 97:6525–6535. doi:10.1007/s00253-012-4453-x