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REVIEW ARTICLE

# Biotechnological valorization of lignocellulosic residues from the oil palm industry: status and perspectives

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## Abstract

Lignocellulosic biomass is a raw material appropriate for obtaining a wide variety of value-added products through different technologies. In the oil palm agroindustry, only 10% of the total products are oils. The remaining 90% is represented by lignocellulosic biomass and effluents. As these residual materials have enormous potential to produce bioproducts, several strategies have been proposed to aggregate value for all plant constituents, further supporting the development of the oil palm industry. This review summarizes the advances in using lignocellulosic residues from the oil palm industry to obtain sugars, biomaterials, bio-oils, biofuels, and animal feed. Additionally, it presents and discusses the integration of mushroom-forming fungal cultivation on these lignocellulosic residues to enable value-added products such as enzymes, edible mushrooms, and animal feed. The technologies and products in development indicate the potential establishment of a biorefinery based on oil palm.

**Keywords** Oil palm · Lignocellulose · Mushroom enzymes · Animal feed · Biorefinery · Bioproducts

**Statement of novelty** The oil palm industry generates huge amounts of lignocellulosic residues that can be used as raw materials to produce different value-added products. The main advances in the biotechnological valorization of these residues are related to hydrolysis processes to obtain fermentable sugars for the production of biomaterials, bioethanol, and other chemicals, as well as bio-oils and animal feed. Fungi offer various commercial and biotechnological applications, particularly with regard to the production of mushrooms and in the treatment of plant biomass to obtain products, such as enzymes and animal feed. Opportunities to integrate the oil palm industry and mushroom cultivation for the bioconversion of wastes into products are developing. The recent research progress in the valorization of oil palm residues supports the integration of several processes in a biorefinery scheme.

### Abbreviations

| | |
|---|---|
| EFB | Empty fruit bunch |
| KS | Kernel shell |
| MF | Mesocarp fiber |
| OPDC | Oil palm decanter cake |
| OPF | Oil palm fronds |
| OPKC | Oil palm kernel cake |
| OPT | Oil palm trunks |

## 1 Introduction

Bio-based processes have been developed to substitute processes based on fossil resources, reducing the environmental impact caused by fossil fuels such as oil, gas, and coal, and enabling the reuse of biological waste from industries. In this context, several groups have been working in the development of processes and treatments of lignocellulosic biomass to generate intermediate chemicals such as sugars, phenols, and organic acids that will subsequently be upgraded to chemicals or biofuels [1, 2].

The carbohydrate in biomass can be employed for the synthesis of numerous chemical products, such as bioethanol and several other compounds that can be applied in the chemical, food, and pharmaceutical industries, including

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ethylene, propylene glycol, 1,4 –butanediol, polylactic acid, acrylic acid, ascorbic acid, polyisoprene, xylaric/xylonic acids, polyols, and methyl tetrahydrofuran, which serve as raw material in the production of plastics, resins, solvents, coatings, adhesives, rubber, and additives [3–5]. The lignin moiety can also be employed as raw material in the production of absorbents, fertilizer releasers, emulsifiers, chelating agents, bioplastics, and in the construction of energy storage devices [6].

The oil palm industry is mainly based on the extraction of oil for different applications. However, the environmental concerns and the different opportunities to aggregate value to residues in this chain are important to consider. This agroindustry produces high amounts of plant, mineral, and liquid residues following harvesting and milling processes. A total of 90% of the production generated corresponds to solid and liquid waste, 80% of which is lignocellulosic biomass (Fig. 1). During the last two decades, research has focused on the development of sustainable applications of both liquid and solid residues, ranging from biofuels to fertilizer, charcoal, bioplastics, biocomposites, adsorbents, pulp, animal feed, and mushroom cultivation [7].

Fungi can contribute to maintaining the ecological balance by participating in the decay and recycling of organic matter in the soil, which includes plant material and animal waste. These micro-organisms aid these processes through the secretion of an enzymatic arsenal composed of cellulases, laccases, esterases, and pectinases that break down the structure of the cell wall and membrane of plants and animals [8, 9]. During decay and recycling, simpler molecules are released in the microenvironment which serve as nutrient sources for fungi and which ultimately, through release into the biosphere, enrich the soil and favor plant growth [10].

The potential of fungal-based organic matter degradation has been exploited in various fields of biotechnology, such as in the pretreatment of lignocellulosic biomass to obtain value-added products [11, 12]. Macrofungi or mushrooms (belonging to fungal classes that produce visible sporocarps) have been exploited historically as foods and as medicinal sources. However, there is now growing interest in the application of macrofungi for value aggregation of plant biomass residues through the generation of different chemical products within a biorefinery scheme. This lignocellulosic biomass, of different structures and compositions, can be used for the cultivation of edible mushrooms. As a result of such cultivation, it is also possible to obtain further products of high added value such as enzymes, bioactive molecules, fermentable sugars, and animal feed.

Palm oil production globally resulted in 71.4 M tons of oil in the 2021 [13], which represents only 10% of the total

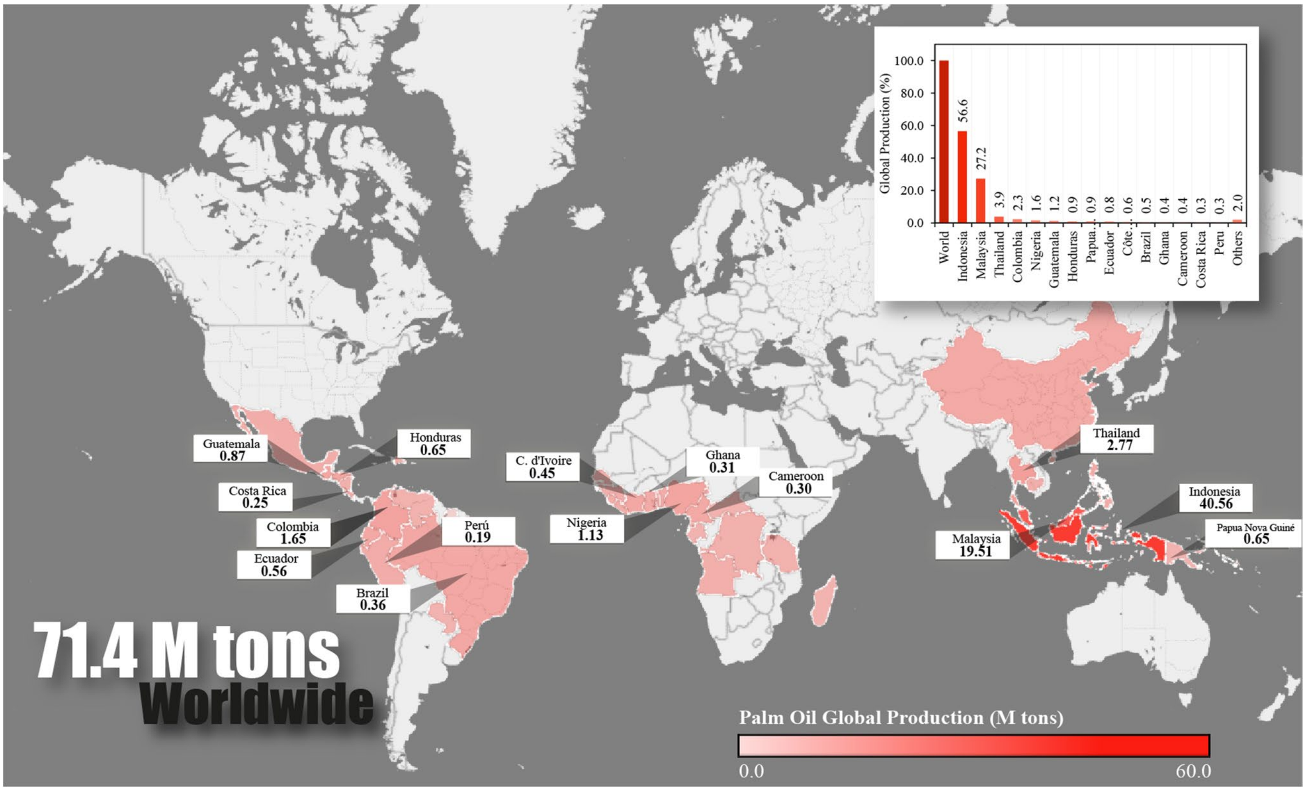

**Fig. 1** World production of palm oil. The data of the 15 countries with the highest production are shown in Megatons and percentile of global production (insert). Data were obtained from FAOAST [18]

plant biomass involved in the entire production process. This indicates that in countries with significant palm oil production such as Indonesia and Malaysia in Asia or Colombia and Brazil in South America, oil palm residues are high, which could become environmental liabilities of considerable impact. As such, it is necessary to develop and implement strategies for the application of waste beyond the usual practices of burning or composting. In this review, given that integration of production practices from different industrial sectors with green technologies is a necessity for the future, the focus is given to the valorization of plant residues from palm oil production in different aspects of biotechnology, mainly with regard to obtaining value-added products such as edible fungi, bioactives, and enzymes. Focus is also given to the opportunities of Spent Mushroom Substrate as animal feed in a biorefinery scheme.

This review is divided into five sections. The first section consists of a brief description of the oil palm industry, emphasizing its performance as an industry in recent years, and the main aspects of processing, production, and waste generation. The second section deals with the current uses of each of the plant residues explained from a biotechnological context. The third section focuses on the production of enzymes from fungal cultures cultivated on waste plant material from the industry as a carbon source. The fourth section seeks to explore the possibilities and advantages of using oil palm residues as a substrate for mushroom cultivation. Finally, in the fifth section, we expose the potential of using the oil palm residues in Spent Mushroom Substrate for animal feed.

## 2 The oil palm agroindustry

Oil palm (*Elaeis guineensis*) is one of the main agricultural cash crops cultivated across the world's tropical regions, with efficient oil extraction from fruit mesocarp and kernel material representing the basis of the macroeconomy for numerous African and Asian countries [14, 15]. In Brazil, "dendê-culture" is in expansion and represents a promising resource for the local economy. The industry is restricted mainly to the north of the country, particularly the state of Pará, with the Northeast region in the state of Bahía also responsible for considerable production [16]. These regions offer favorable climatic conditions for crop production, with high precipitation and uniform solar radiation.

Palm oil is used mainly in the food industry (85–90% of total produced), due to its physicochemical characteristics as high solid fat content, high oxidative stability, high and/low melting, and crystallization properties of triacylglycerols, in addition to its constant supply and competitive price [17]. Palm oil is a raw material for the manufacture of foods such as shortenings, margarine, oils for frying, salads, candies, ice creams, and infant formula. Palm oil can be also employed in the manufacture of dietary supplements such as vitamins, carotenoids, and phytosterols, in the preparation of non-food products such as surfactants, and as a building block for the synthesis of other chemicals, such as fatty acids, fatty alcohols, methyl esters, and fatty amines. According to the United States Department of Agriculture [13], the world's production of palm oil reached 71.4 million metric tons in 2018, in response to needs in the production chains.

### 2.1 Palm oil production and uses worldwide

Crude palm oil is globally the most important vegetable oil, in terms of production and consumption. In 2021, CPO production reached 71.4 M tons worldwide [13], with production currently concentrated in South-East Asia (Fig. 1), where Indonesia and Malaysia are the major producers and responsible for 85.37% of world production. South America is the second-highest producing region, particularly Colombia (1.85 M tons) and Brazil (0.45 M tons) (Fig. 2).

In Brazil, palm oil production has been increasing during the last 70 years, with this trend expected to continue. In 2019, Brazil ranked ninth globally in terms of palm oil [18], producing 2.583.293 tons of oil palm fruit and 400,560 tons of CPO (Fig. 2). In terms of consumption, however, the country is ranked only in 31st place, behind countries such as China, India, and the USA, which together account for 47.9% of global imports. Globally, an estimated 233.82 Mha of fertile land is potentially suitable for oil palm cultivation. Brazil has the largest potential area with 44.3 Mha (or 18.6% in the world), excluding lands of high environmental value and those applied to agricultural uses such as pasture or cropland [19]. As such, there is considerable potential for sustainable expansion of the palm oil agro-industry in Brazil.

Oil palm is the second most widely produced oil crop in Brazil after soybean. Cultivation occupies approximately 140.000 ha, with production divided across large-scale agroindustry plantations, as well as medium-scale and smallholder plots, where bunches are sold to agroindustries for processing [15].

### 2.2 Oil palm processing

Oil palm processing begins at the 3-year stage when palms produce approximately 16 bunches annually. A schematic version of the process is detailed in Fig. 3. Processing of fresh fruit bunches (FFB) begins with the sterilization of bunches, at 140 °C, to destroy oil-splitting enzymes and to arrest hydrolysis and autoxidation. This treatment also weakens the fruit stem and facilitates removal from bunches. This FFB processing generates most of the Palm Oil Mill Effluent (POME), a liquid waste with significant amounts of organic

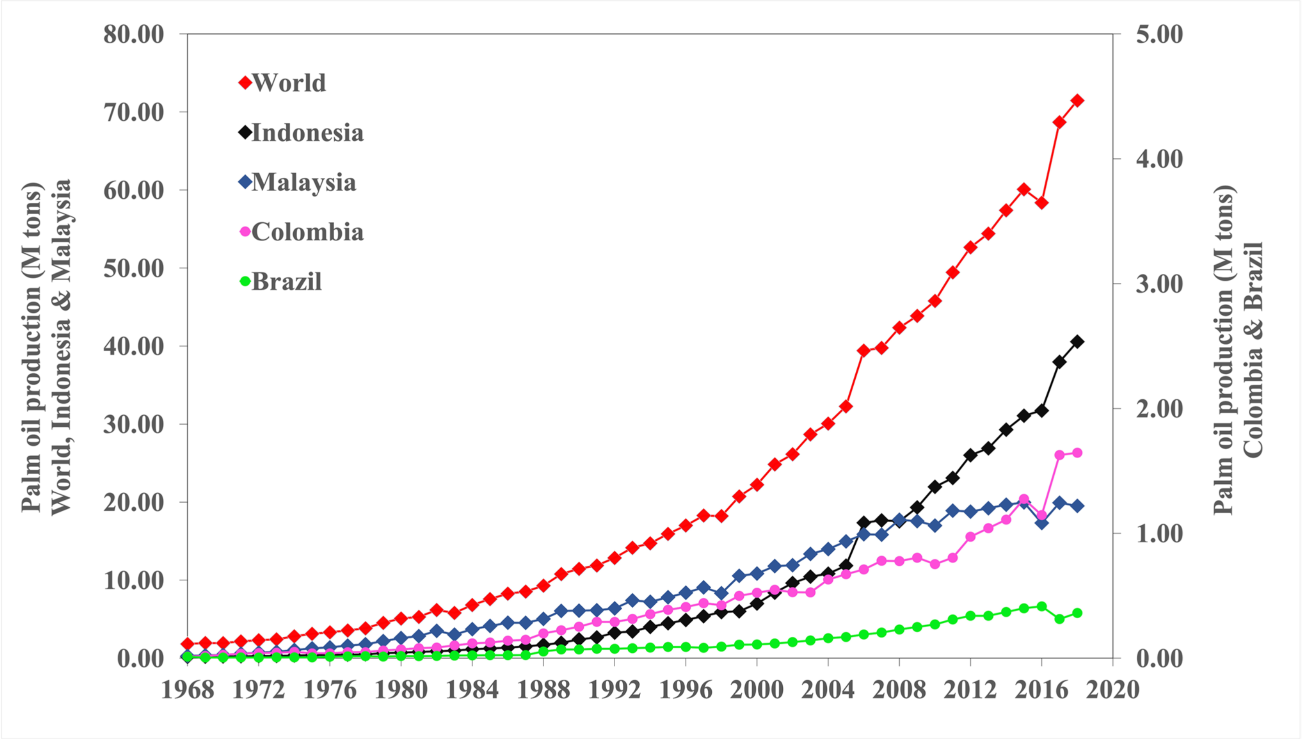

**Fig. 2** Evolution of palm oil production over time

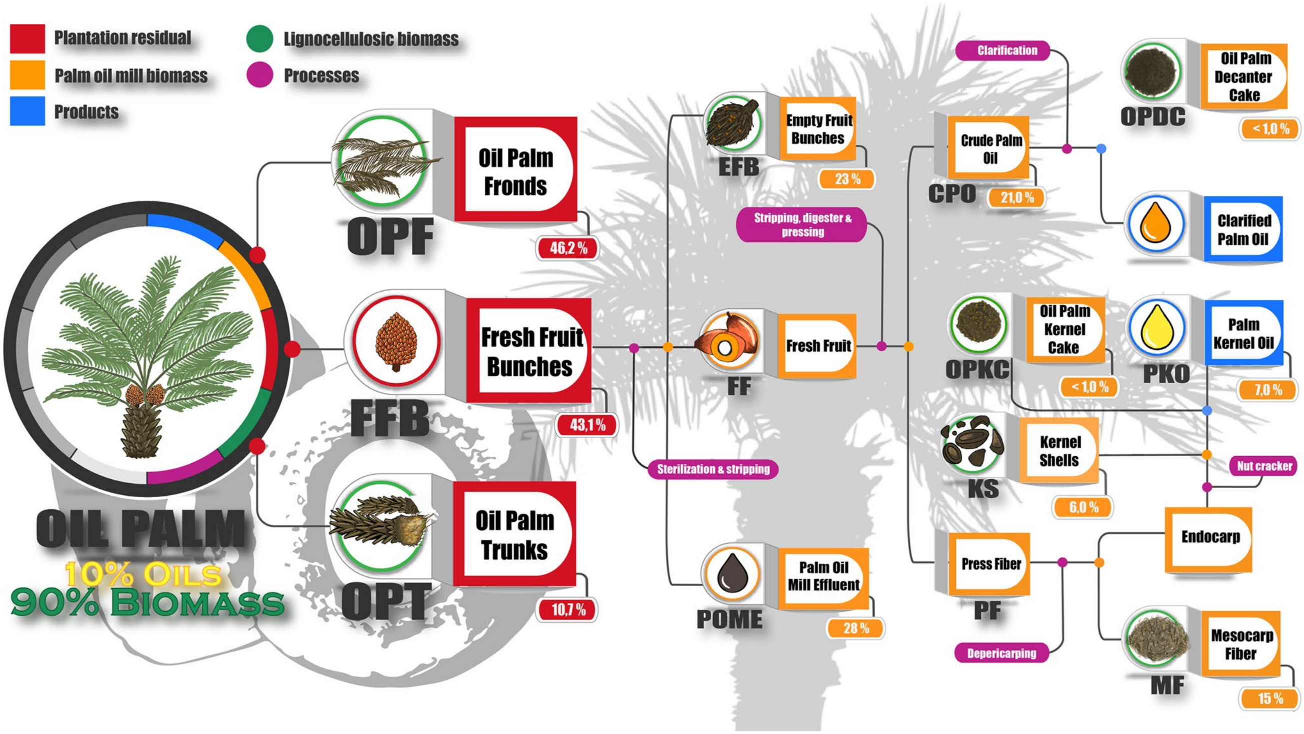

**Fig. 3** Production chain for the oil palm industry, with main products and residues from the plantation and milling processes. Percentages correspond to calculations based on the dry weight, according to [188]. The subdivision of the percentages of the biomass generated in the plantations is detailed in red boxes. The subdivision of the percentages of biomass generated in factories or mills is detailed in orange boxes (wastes) and blue boxes (products/oils)

matter [20]. FFB are then transported to a threshing drum where the fruits are separated from bunches, which, then are referred to as Empty Fruit Bunches (EFB), representing the first lignocellulosic residue of the oil palm mill processing (Fig. 3). Fruits are subsequently transferred to digesters and pressing machines to extract the Crude Palm Oil (CPO), where mesocarp fiber (MF) is generated as a second lignocellulosic residue (Fig. 3). Crude oil is decanted and centrifuged to clarify the oil by separating particles and water, producing a "cake" formed as sediment (Oil Palm Decanter Cake, OPDC), the third lignocellulosic residue. The endocarps separated from pressed fruits are cracked to obtain the kernel, then used to produce the Palm Kernel Oil (PKO) (Fig. 3). The Kernel Shells (KS) and Oil Palm Kernel Cake (OPKC) represent further lignocellulosic residues. Both CPO and PKO are then transported to refining processes to reduce undesirable compounds that include heavy-metal traces, phosphatides, and free fatty acids [21].

## 3 Current practices and applications of oil palm lignocellulosic biomass residues

Lignocellulosic biomass is today associated with the production of clean energy, either in form of sugars for fermentation to biofuels or different types of bioproducts. Thus, plant residues previously underutilized are now a commodity for different market platforms. Depending on the variety of composition and technologies, bio-based chemicals with high added-value can be obtained from lignocellulosic biomass, and potentially shifting consumption away from petroleum-based chemicals [22]. Lignocellulosic biomass consists of a hetero-matrix mainly of the carbohydrate-based polymers cellulose and hemicellulose, together with the phenolic macromolecule lignin. A detailed description of the molecular structure of lignocellulosic biomass can be found in Bajpai [23]. The structural composition of oil palm residues can vary, depending on the type of biomass, as detailed in Table 1.

To efficiently utilize plant biomass as an energy source, it is, therefore, necessary to fractionate the major components into monomers or to separate those components by breaking molecular linkages. Biomass deconstruction to release the sugars requires sequential pretreatment and hydrolysis steps, which can be grouped as physical, chemical, biological, or combinatorial approaches [11, 24]. Pretreatment principles and approaches were recently reviewed in Shirkavand et al. [25] and Kumar & Sharma [26]. Approaches vary in function of the composition of plant biomass, with, for example, steam explosion typically used with hardwoods, whereas lime pretreatment is more appropriate for softwoods or biomass with high lignin content. Considerable research is underway into the integration of different methods to increase the performance of individual processes. Such pretreatment approaches should also ideally offer high lignin removal, low hemicellulose/cellulose loss, and low operational costs in terms of energy and capital input at an industrial scale. Methods employed should also guarantee an absence of accumulation of toxic compounds or inhibitors of hydrolysis and fermentation [27]. Under such approaches, the integration of biomass pretreatment in biorefineries has been proposed as a promising route to coordinate different biotechnological methods and agricultural practices, enabling production not only of sugars and biofuels but also biochemicals and biopolymers [28, 29].

Oil palm lignocellulosic residues correspond to 90% of the total biomass generated in oil palm cultivation, with oils representing only 10% (Fig. 3) [30]. Currently, oil palm byproducts are used in several agricultural practices or converted into added value via the conversion technologies [31]. Examples of these added-value products are summarized in Table 2.

### 3.1 Trunks and fronds

Trunks and fronds differ from other lignocellulosic residues in that they are generated in the field when FFB is harvested. A total of 25–30 years after planting, plant productivity decreases significantly, such that replanting of the next generation of seedlings is required. During replanting, felled oil palm trunks (OPT) may be left to decompose in the field, contributing to soil conservation, erosion control,

**Table 1** Structural composition of lignocellulosic residues of the palm oil industry. All values are presented as a percentile of dry weigh

| Oil palm lignocellulosic biomass | Cellulose | Hemicellulose | Lignin | Ashes | Extractives | Ref |
|---|---|---|---|---|---|---|
| OPF | 28.7–42.8 | 12.5–26.02 | 19.7–37.6 | 0.2–5.8 | 7.64–22.2 | [43, 173, 174] |
| OPT | 41.1–56.1 | 16.5–34.4 | 11.7–19.11 | 3.4 | 0.5–19.1 | [38, 175, 176] |
| EFB | 44.4–59.7 | 22.1–30.9 | 14.2–18.1 | 2.8–5.4 | 0.1 | [177, 178] |
| KS | 29.7–33.04 | 18.0–23.8 | 45.6–53.4 | 1.1–6.7 | 9.8 | [179] |
| OPKC | 35.55 | 30.81 | 22.6 | 4.47 | 6.82 | [163] |
| MF | 23.0–40.12 | 12.9–28.2 | 25.2–36.0 | 1.4–9.0 | 5.2–10.0 | [94, 180] |
| OPDC | 16.8 | 5.8 | 17.4 | 9.2 | 10.5 | [94] |

**Table 2** Added-value products or chemical blocks obtained through biotechnology process using oil palm lignocellulosic biomass as raw material

| Oil palm lignocellulosic biomass | Added-value products | References |
|---|---|---|
| Oil palm trunks (OPF) | Ethanol (via fermentation) | [41] |
| | Succinic acid (via fermentation) | [42, 43] |
| | Furfural | [44] |
| | Microcrystals of cellulose | [181] |
| | Activated carbon | [46] |
| Oil palm fronds (OPT) | Ethanol (via fermentation) | [34] |
| | Succinic acid (via fermentation) | [33] |
| | Bio-oil | [36, 37] |
| | Nanocrystals of cellulose | [38] |
| | Natural adhesives | [40] |
| EFB | Sugars (via hydrolysis) | [50] |
| | Ethanol (via fermentation) | [52] |
| | Activated carbon | [53] |
| | Bio-oil | [54–56] |
| | Nanocrystals | [58] |
| | Acoustic absorbers | [59] |
| | Bio compost | [60] |
| Kernel shells (KS) | Bio-oil | [71, 72] |
| | Activated carbon | [71] |
| | Concrete aggregate | [76] |
| Oil palm kernel cake (OPKC) | Animal feed | [77, 81–84, 86] |
| Mesocarp fiber (MF) | Sugars (via hydrolysis) | [65–68] |
| | Bio-oil | [180] |
| | Bio-char | [180] |
| | Antioxidants (α-tocopherol and β-carotenes) | [69] |
| | Antioxidants (phenolic compounds) | [70] |
| Oil palm decanter cake (OPDC) | Composting | [89] |
| | Metanol | [91] |
| | Biohydrogen | [90] |
| | Butanol | [92] |

and nutrient supply. Alternatively, OPT can be burned and ashes applied in mulching. Both scenarios, however, can present negative impacts in terms of obstructing replantation, favoring insect pests and pathogen inoculum build-up, and increasing carbon emissions [32]. Potentially more energy-efficient applications of OPT have, however, now been described. As sap represents up to 70% of the total weight of OPT, its conversion, by naturally present enzymes, into monosaccharides such as glucose, fructose, sucrose, and galactose, for example, offers considerable potential in biomass applications [33].

OPT pressing results in solid residues that contain up to 49% glucans. Prawitwong et al. [34] described ethanol production from parenchymatous and vascular tissue residues following OPT pressing. High solid-state simultaneous saccharification and fermentation (HSS-SSF) using amylase and cellulase enzymes for hydrolysis and *Saccharomyces cerevisiae* for fermentation enabled a yield of up to 76.7% of the maximum theoretical ethanol yield. Sugars obtained from pretreated and hydrolyzed OPT have also been used in fermentation by *Actinobacillus succinogenes* and the production of succinic acid, an important chemical in markets of bioplastics, coatings, pharmacy, food, and pigments [35].

OPT can also be used in the production of bio-oil, a dark brown liquid comprised of highly oxygenated compounds that can be produced after depolymerization and fragmentation of structural components of the cell wall with a rapid increase of temperature [36]. Bio-oils are currently used to improve soil quality, eliminate pests, and control plant growth. Oramahi et al. [37] investigated the effect of pyrolysis conditions for obtaining higher amounts of bio-oil from OPT. The optimal conditions were 456.1 °C, 139.98 min, and 9.26% of moisture present in the pyrolysis process. OPT has also been used to obtain cellulose nanocrystal. Lamaming et al. [38] obtained nanocrystals of 7.67–7.97 nm in diameter and 397.03–361.70 nm in length after acid hydrolysis. Nanocrystals of cellulose have several applications, including in enzyme immobilization, drug/gene delivery, biosensors, adsorbents, supercapacitors, emulsion stabilizers, and nanocomposite components [39]. Finally, potential natural adhesives from the starch of OPT were evaluated by Choowang and Luengchavanon [40]. According to the authors, the dry powder obtained from the core zone of OPT could bond rubberwood veneer, with the water resistance increased by blending the powder with citric acid.

Oil palm fronds (OPF) are produced daily, throughout the year, following palm pruning. Two hundred and fifty (250) million metric tons of OPF are produced globally and correspond to 46.2% of overall oil palm biomass. OPF is typically applied in fields in the same way as OPT, either as fertilizers or burned to produce ash [32]. The vast quantities of OPF (approximately 82.5 kg fronds/palm/year) offer the potential for use as a value-added raw material.

Alternative uses of OPFs can include the production of fermentable sugars for conversion to ethanol. For example, Kumneadklang [41] used both acid ($H_2SO_4$) and alkali-based (NaOH and NaOH in $H_2O_2$) pretreatments of OPF for simultaneous saccharification and fermentation using cellulase Cellic® Ctec2 (Novozymes) to enable hydrolysis of pretreated OPF and employment of the yeast *S. cerevisiae* to ferment sugars to ethanol. Following fermentation, the maximum ethanol concentration achieved was 17.2 g/L, obtained with OPF pretreated with NaOH in $H_2O_2$ and 56.9 g/L of sugars.

In addition to bioethanol, sugars and other components obtained from OPF can be used for other biotechnological purposes. For example, a total of 40 g/L of sugars including glucose, fructose, sucrose, and fructose were obtained from one portion of fronds (1–3 m from the base of the petiole), where 73% of sugars were used for *A. succinogenes* to produce succinic acid [42, 43]. In Lee et al. [44], OPF was pretreated with an ultrasonic probe and aqueous choline chloride-oxalic acid to produce furfural, reaching a yield of 56.5% (based on xylose concentration from hemicellulose). Furfural is a versatile chemical that can be used in fuels, solvents, pharmaceuticals, materials, and as a chemical intermediate.

The cellulose fractions of OPF pulps have been employed to obtain microcrystalline cellulose (MCC) and activated carbon as a potential adsorbent to methylene blue and herbicides, respectively [45, 46]. Also, isolated lignin was tested to improve solubility and antioxidant properties of the organic scavenger *p*-nitrophenol [47]. Another application of OPF is as animal feed. In Rahman et al. (2011) the digestibility of fronds was improved after white-rot fungi colonization with the fungal species *Ceriporiopsis subvermispora* and *Phanerochaete chrysosporium*, which lead to a decrease in lignin content and partial degradation of cellulose.

## 3.2 Empty fruit bunches

The EFB have been used to generate energy for milling following incineration. Nevertheless, the high moisture content of around 60% makes this residue unsuitable for burning, such that it is generally dispensed in plantations [49]. Given this limitation, alternative applications of EFB have now been evaluated. The release of fermentable sugars from pretreated and hydrolyzed EFB was recently evaluated by different authors. In Palamae et al. [50], EFB was pretreated with paracetic acid/alkali peroxide and then used to produce monosaccharides through enzymatic hydrolysis. Pretreated biomass generated 629.8 g of glucose per kg of dry biomass, in contrast to hydrolysates of raw EFB that generated 3.0 g. Cui et al. [51] reached a value of 85.2% of polysaccharide conversion (83.6 $g.L^{-1}$) after 72 h of hydrolysis by using cellulases for EFB pretreated with $Ca(OH)_2$ and formic acid. These fermentable sugars obtained from oil palm biomass can be applied in bioethanol production; an example of this was carried out by Kamoldeen et al. [52], where EFB pretreated with mild alkali conditions allowed the total production of 418.9 $L.tonne^{-1}$ or 33% ($w.w^{-1}$) ethanol yield of treated EFB after co-fermentation of glucose and pentose by *S. cerevisiae* and *Pichia stipites*, respectively.

In addition to being a source of fermentable sugars, EFB has been described as a potential substrate for technologies enabling the generation of additional bioproducts. For example, Osman et al. [53] developed a statistical model to obtain higher quantities of activated carbon from EFB through a pyrolysis process. The authors claimed that the treatment of EFB through this pyrolysis method is a potentially inexpensive alternative to obtain activated carbon. In this context, the bio-oil production from EFB using pyrolysis was also demonstrated in several studies (CHANG, 2014; VECINO MANTILLA et al., 2014; YIIN et al., 2014). For example, fast pyrolysis was carried out to obtain bio-oils from EFB by testing various temperatures (400, 500, and 600 °C); with maximum bio-oil content obtained at 500 °C, with 27% conversion yield, and a bio-oil composed mainly of lauric acid [57].

EFB has also been used to produce sustainable bioproducts such as cellulose nanocrystals [58], acoustic absorbers [59], and bio compost [60]. In addition, a few recent examples are applying EFB as animal feed. Some studies demonstrated a promising result by using mushrooms such as *Pleurotus sajor-caju* and *Coprinus cinereus* as lignocellulosic degraders, which increase the ruminal digestibility by decreasing the crude fiber. This also increases the protein content in the substrate and enables the production of edible mushrooms, which will be discussed in more detail later [61]. A more recent study evaluated the use of different edible mushrooms to increase the digestibility of lignocellulosic biomass for animal feed [62]. Thus, there is a potential opportunity to integrate the edible mushroom industry and animal feed production by using this type of vegetable material, especially EFB, as it represents 23% of the biomass residues in the milling process (Fig. 3).

### 3.3 Mesocarp fiber

MF is generated from pressing fruits to obtain palm oil. Usually, one ton of fresh fruit bunches (FFB) produces 0.12 tons of Mesocarp Fiber (MF). The MF is collected and used in boilers to produce energy, and more sparingly as organic fertilizer in plantations. In the biorefinery context, MF is today lignocellulosic biomass produced from palm oil processing with only a limited number of studies reported on the application in obtaining bioproducts [63]. With appropriate thermochemical treatment, however, the chemical composition of MF offers potential for exploitation. This assumption includes, for example, the extraction of bio-oils and biochar in pyrolysis reactions. Kabir et al. [64] obtained 47% bio-oils and 53% of biochar/gases from MF decomposition by pyrolysis performed at 550 °C, mainly composed of carbonyl and aromatic groups. In addition, oil palm MF has also potential as a fermentable sugar supplier. In Zakaria et al. [65] cell wall breakdown of MF was conducted with a combinatorial ball milling and thermochemical pretreatment, enabling a reduction of cellulose crystallinity and lignin content, and maximum glucose and xylose yields of 62.9% and 46.5%, respectively. Other studies have also proposed the release of sugars following MF pretreatment and hydrolysis processes [66–68]. These results indicate that MF is a promising lignocellulosic source to produce biofuels and other chemicals.

MF has also been considered as a raw material for the production of bioactive molecules [69]. In this context, ultrasound-assisted extraction has been used to obtain carotene and α-tocopherol. In addition to α-tocopherol and β-carotenes, the extracts, which possess high antioxidant and high sun protection activity, included the molecules squalene and β-sitosterol. Thus, MF has been considered as a source to produce molecules for use in the cosmetic and pharmaceutical industries. Additionally, the bioactivity of MF extracts may also be used as antimicrobial agents, including for the control of certain important phytopathogenic fungi affecting oil palm production. In condensed extracts from MF pretreated with Superheated Steam (SHS) at 240 °C, for example, a total of 62 molecules were identified, comprising mainly furans, phenolic, and acids [70]. The occurrence of phenolic compounds such as 4-methylbenzoaldehyde, 2,5-dihydroxybenzaldehyde, and 2-methoxyhydroquinone may explain the effective antifungal activity against *Ganoderma boninense*, which is the causal organism of basal stem rot, an important disease of oil palm in S.E. Asian and Pacific plantations.

### 3.4 Kernel shell and oil palm kernel cake

Kernel Shells (KS) and Oil Palm Kernel Cake (PKC) are produced after the separation of fruit endocarp and mesocarp, respectively, during the milling processes. The KS corresponds to the endocarp portion of fruits and traditionally is used in steam boilers as an energy source. KS has been used to produce added-value bioproducts such as bio-oils with high phenolic compounds, glycerides, and fatty acids [71, 72], and activated carbon which is used as an absorber of toxic wastewater chemicals such as dyes (basic blue 9, remazol black 5, and methylene blue), copper, lead, and nickel [73–75]. The KS has also been extensively employed as lightweight concrete aggregate, as reviewed in Alengaram et al. [76]. This biomass has comparable characteristics to conventional aggregates and is highly suitable as concrete aggregate in asphalt preparations, with high potential in pavement construction in rural zones.

Unlike the kernel shells, Oil Palm Kernel Cake (OPKC) has been investigated as a supplement in animal feed, particularly for the ruminants [77]. Protein content (≥ 15%) is the most attractive feature for this purpose. Sixteen amino acids have been characterized in OPKC, where arginine and glutamic acid account for the higher percentage [78]. These two amino acids play various roles in the animal, including regulatory function, immune response, DNA and protein synthesis, body-weight gain, antioxidant effect, and cell proliferation [79, 80]. These functions are relevant in the choice of dietary supplements to increase the performance of the animal, with OPKC representing a potential resource in the feed not only for ruminants but also for monogastric species.

OPKC as a dietary supplement ranges between 10 and 30% as a substitute for conventional formulas in feeding, with no significant differences in the performances of broiler chickens, grazing lambs, and pigs when compared with other conventional crops [81–84]. In addition to carbohydrates and proteins, OPKC provides animal feed formulations with a large number of polyunsaturated fatty acids (e.g., omega-3) [82]. However, OPKC intake is related to low digestibility in ovine, swine, and bird species due to the high non-starch carbohydrate and lignin content. This, however, can be resolved using strategies such as fermentation and enzymatic treatment of OPKC, with promising results observed in the improvement of nutritive value. For example, *Paenibacillus polymyxa* was used in solid-state fermentation prior to broiler chickens feeding, improving nutrient digestibility compared with control and non-fermented OPKC [85]. Similar results were observed in swine and poultry chickens fed on OPKC treated with enzymes such as cellulases, xylanases, mannanases, and phytases, increasing nutrient availability [83, 84].

Despite the successful application of OPKC in animal fed, some authors argue that it possesses low nutritive value because of the lack of amino acids like lysine, tryptophan, and methionine and lesser protein percentage compared with other feedstocks [86]. Considering this, different alternatives to using OPKC in the biorefinery context have been evaluated. One of the strategies is based on the application of the high carbohydrate content ($\geq 50\%$) to produce bioethanol. Among the carbohydrates, mannan is approximately 20% of total OPKC polysaccharides and can be converted from mannose to ethanol via fermentation by *S. cerevisiae*. This process can yield 90% of conversion to ethanol and induces a more concentrated protein product, which is interesting with regard to the use as an animal feed [86]. In contrast, the use of OPKC sugars to produce butanol is less advantageous, since the major butanol fermenting bacteria (e.g., *Clostridium*) typically prefer glucose rather than mannose [87, 88].

### 3.5 Oil palm decanter cake

OPDC is obtained after the crude palm oil clarification process. Weight represents approximately 4–5% dry weight or 42 kg per ton of fresh fruit bunches. In practice, OPDC is generally dispensed in plantations or mixed with other oil palm lignocellulosic residues such as MF, KS, and OPKC for subsequent disposal in boilers. OPDC has high organic matter content and lipid residues of mesocarp extraction, so are highly suitable for use in composting, animal feed, and biogas production [89–91]. The structural carbohydrate content of OPDC also makes this residue suitable for the production of lignocellulolytic enzymes, which can then be applied to obtain sugars that can be fermented to produce polyose, biobutanol, and bioethanol [92–94].

## 4 Mushroom-derived enzymes produced on oil palm residues

Mushrooms are capable of growing in a great diversity of lignocellulosic materials [95–97]. In nature, they produce enzymatic complexes to degrade vegetal constituents, releasing nutrients for uptake via hyphae and distribution within the organism [98]. The vegetal constituents degraded include the well-recognized cellulose, hemicellulose, lignin, and pectin, as well as molecules related to antinutritional effects in animal feed. Furthermore, mushrooms secrete primary and secondary metabolites during the growth phase, which may be biologically active [99, 100]. These activities increase the nutritional value of potential plant-derived feed to animals, particularly those that are unable to naturally decompose specific vegetal constituents.

Fungi produce a mixture of enzymes (cellulases, hemicellulases, esterases, and oxidases) to degrade the large and recalcitrant polymers of lignocellulose to simple monosaccharides and phenolic derivates [101, 102]. This process is also referred to as biological pretreatment and is the basis for using biomass to produce biofuels, chemicals, animal feed, or bioremediation mediators. Biological pretreatment is an eco-friendly process with no release of toxic compounds and low energy input requirements, with the potential to contribute to the reduction of greenhouse gas emissions and stimulation of rural economies [103]. Currently, the enzyme-catalyzed processes are gradually replacing chemical processes in many areas of industry, and at this point, several methods have been developed to improve the properties of known enzymes and to identify and synthesize new enzymes [103]. Macrofungi, including mushrooms, are recognized as high producers of several types of enzymes [104]. Thus, the biological pretreatment of lignocellulosic biomass can be coupled with the production of enzymes of industrial interest, such as those employed in industries of detergent (proteases, cellulases, lipases, and oxidoreductases), textile (laccases and cellulases), paper, and pulp (cellulases and xylanases), leather treatment (proteases and lipases), animal feed (xylanases, cellulases, and phytases), and food preparation (pectinases, cellulases, proteases, and oxidoreductases) [105].

In this context, residual lignocellulosic biomass from oil palm has been used as a substrate for the cultivation of mushrooms for biological pretreatment and enzyme production (Fig. 4), mainly using EFB (Table 3). In Widiastutu et al. [106], EFB was used as a growth substrate for mushroom species *Omphalina* sp. and *Pleurotus ostreatus*, for the production of ligninolytic activities during solid-state fermentation. Laccase (LAC), manganese peroxidase (MnP), and Lignin peroxidase (LiP, in *P. ostreatus* only) activities were greater during the somatic phase of both fungi, decreasing during the formation of fruiting bodies. EFB was also used to culture *Trametes lactinea* and *Pycnoporus sanguineus* [107]. In this work, both fungi were able to produce lignocellulolytic enzymes growing only in EFB; however, this substrate enhanced *P. sanguineus* enzymatic activities MnP (42.51 U $\text{mg}^{-1}$ protein), LiP (103.20 U $\text{mg}^{-1}$ protein), and carboximetilcellulase (34.39 U $\text{g}^{-1}$ protein) (Table 3).

Certain mushroom species within the Basidiomycete class are usually related to the phenomenon of white rot, which is characterized by the ability of the fungus to decompose plant cell walls and reduce lignin content through the activity of oxidative enzymes such as LiP and laccase. The structural characteristics of EFB, presumably also due to the high content of holocellulose, induce mushrooms to produce these types of enzymes [108], increasing digestibility. Indeed, the high ligninolytic enzyme production by mushrooms may also lead to a high degradation of lignin content, and subsequently, increased biodegradability. For example, in Mamimin et al. [95], *Volvariella volvacea* secreted laccase and hemicellulase activities in its growth phase, which led to a reduction in the percentage of lignin and hemicellulose

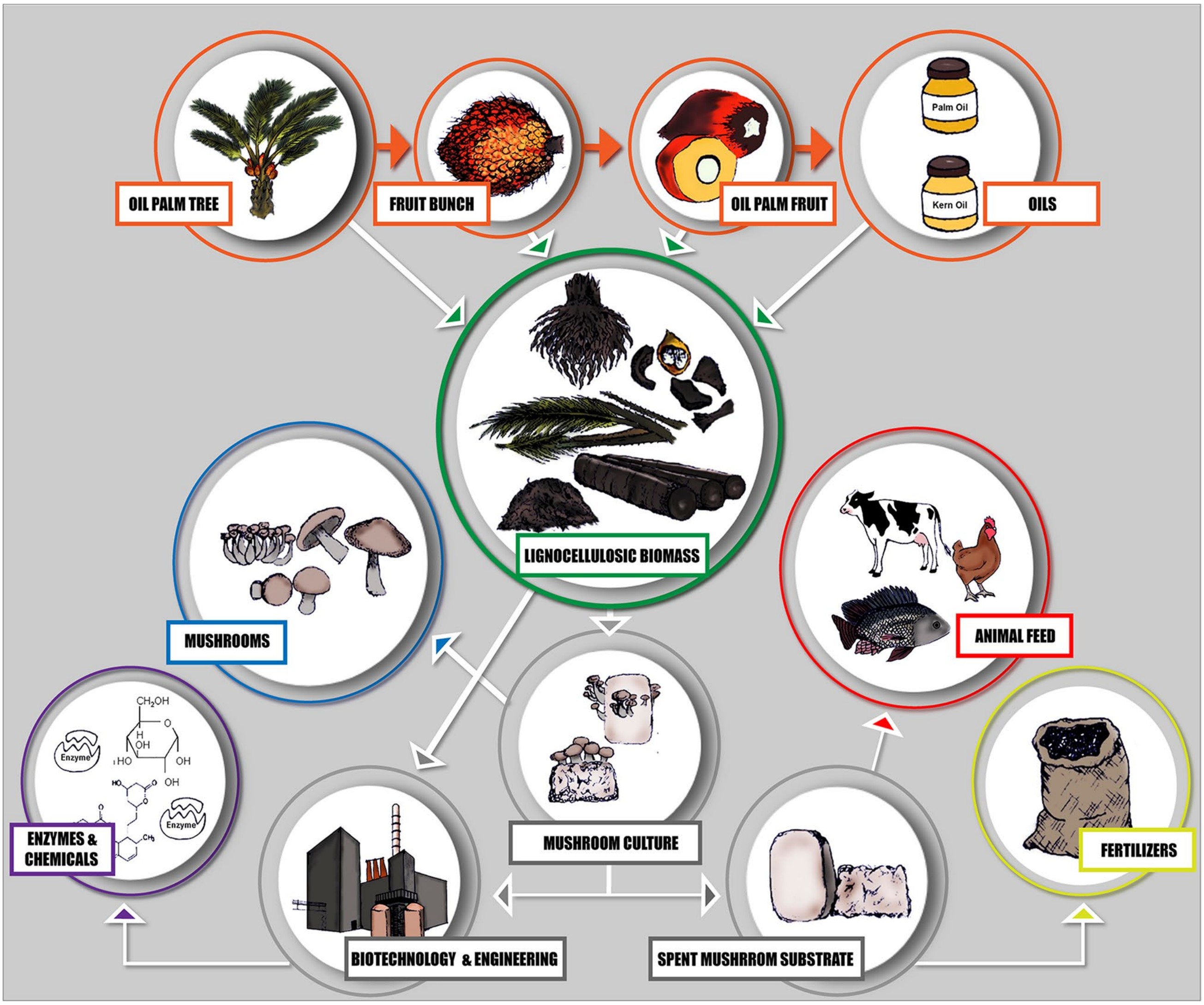

**Fig. 4** The oil palm agroindustry is a biorefinery model to obtain new products from oil palm processing. Palm oil processing and main products, orange circles; lignocellulosic biomass generated in the different stages of oil processing, green circle; lignocellulosic biomass used as a substrate to mushroom cultivation, which generates spent mushroom substrate and at the same time, raw material for use in biotechnology and engineering, gray circles. Main potential bioproducts of the integration of the oil palm industry and fungi culture: edible mushrooms (blue), animal feed (red), enzymes and chemicals (purple), and fertilizers (yellow)

in EFB. This reduction enabled greater access of bacteria to the cellulose fibers, and subsequently, the production of biogas (methane) by anaerobic digestion.

Although OPT and OPF are the two lignocellulosic residues generated in the field (Fig. 3), their use as a substrate for enzyme production is scarce. OPT has been used as a substrate for the growth and production of lignocellulolytic enzymes and bio pulping by *Trametes versicolor* in submerged fermentation [109]. Here, ligninolytic enzyme activity was detected with laccases (218.6 U $L^{-1}$), MnP (134.2 U $L^{-1}$), and LiP (94 U $L^{-1}$), but with less xylanase and cellulase activity. *T. versicolor* was evaluated recently for the production of ligninolytic enzymes using different agro-industrial wastes such as sugarcane bagasse, vinasse, barley bagasse, and white sludge [110]. The results showed a range of laccase activities between 100 and 1600 U.$L^{-1}$, which indicates that OPT is a suitable carbon source for the production of ligninolytic enzymes. OPF was also used as a substrate to obtain laccases using the medicinal mushroom *P. sanguineus,* with maximum production values of 403 U. $Kg^{-1}$ [111] and 7600 U. $Kg^{-1}$ [112] of parenchyma tissue.

The OPDC, despite being less easily available than other lignocellulosic biomasses of oil palm, has been the subject of some studies for enzyme production with fungi. In Thamvithayakorn et al. [113], to optimize the production of ligninolytic enzymes from the white-rot fungus

**Table 3** Enzyme production of mushroom species cultivated on lignocellulosic biomasses of the oil palm industry

| Mushroom specie | Maximum enzyme production | Oil palm residue substrate | Type of culture | Ref |
|---|---|---|---|---|
| *P. sanguineus* | • Lacase (< 20.0 U.mg$^{-1}$ protein), 7th day<br>• MnP (42.5 U.mg$^{-1}$ protein), 7th day<br>• LiP (73.23 U.mg$^{-1}$ protein), 7th day<br>• CMCase (34.0 U.mg$^{-1}$ protein), 21st day<br>• Xylanase (22.0 U.mg$^{-1}$ protein), 21st day<br>• Amylase (20.0 U.mg$^{-1}$ protein), 21st day | EFB | Solid-state fermentation | [107] |
| *Trametes lactinea* | • Lacase (500 U.mg$^{-1}$ protein), 7th day<br>• MnP (12.0 U.mg$^{-1}$ protein), 7th day<br>• LiP (57.3 U.mg$^{-1}$ protein), 7th day<br>• CMCase (14.0 U.mg$^{-1}$ protein), 21st day<br>• Xylanase (18.0 U.mg$^{-1}$ protein), 7th day<br>• Amylase (98.0 U.mg$^{-1}$ protein), 21st day | EFB | Solid-state fermentation | |
| *P. ostreatus* | • Lacase (1.76 U.mL$^{-1}$), 3rd week<br>• MnP (0.79 U.mL$^{-1}$), 5th week<br>• LiP (0.78 U.mL$^{-1}$), 4th week | EFB | Solid-state fermentation | [106] |
| *Omphalina* sp. | • Lacase (1.99 U.mL$^{-1}$), 3rd week<br>• MnP (< 0.5 U.mL$^{-1}$ protein), 2nd week | EFB | Solid-state fermentation | |
| *Volvariella volvacea* | • Lacase (0.14 U.g$^{-1}$ EFB), 7th day<br>• Xylanase (0.013 U.g$^{-1}$ EFB), 7th day<br>• Endoglucanase (0.005 U g$^{-1}$ EFB), 7th day<br>• Exoglucanase (0.002 U g$^{-1}$ EFB), 10th day | EFB | Solid-state fermentation | [95] |
| *P. chrysosporium* | • MnP (6.52 U.mL$^{-1}$), 20th day<br>• LiP (17.0 U.mL$^{-1}$), 20th day | OPF | Solid-state fermentation | [182] |
| *P. chrysosporium* | • Laccase (1472 U.L$^{-1}$), 23rd day | EFB | Solid-state fermentation | [183] |
| *Pseudolagarobasidium* sp. | • Laccase (5.84 U.gds$^{-1}$), 7th day<br>• MnP (5.16 U.gds$^{-1}$), 7th day | OPDC | Solid-state fermentation | [113] |
| Isolated fungus Lacc C | • Laccase (1.5 U.mg$^{-1}$), 14th day | EFB | Submerged fermentation | [184] |
| *Marasmius* sp | • Laccase (330.1 U.L$^{-1}$), 8th day | EFB | Submerged fermentation | [185] |
| *Trametes versicolor* | • Laccase (218.6 U.L$^{-1}$), 10th day<br>• MnP (134.2 U.L$^{-1}$), 12th day<br>• LiP (94 U.L$^{-1}$), 12th day<br>• Cellulase (53.34 U.L$^{-11}$), 10th day<br>• Xylanase (1.48 U.L$^{-1}$), 10th day | OPT | Submerged fermentation | [109] |
| *P. sanguineus* | • Laccase (403 U.Kg$^{-1}$ OPFPT), 10th day | OPT<br>Parenchyma tissue | Solid-state fermentation | [111] |
| *Amauroderma rugosum* | • Phytase (8.28 U.gds$^{-1}$), 7th day | EFB | Solid-state fermentation | [186] |

*Pseudolagarobasidium* sp, cultures were grown on OPDC as substrate, and variations in the concentration of components of the medium were performed using a Plackett–Burman design and response surface methodology as statistical tools. Statistical optimization showed the greatest values of laccase and MnP of 5.84 U.gds$^{-1}$ and 5.16 U.gds$^{-1}$, respectively, at 30 °C after 7 days. Recently, Peláez et al. [94] used OPDC for screening monocultures and cocultures of different species of mushroom-forming fungi using 2.5% (w.v$^{-1}$) of OPDC as substrate in submerged fermentation to produce enzyme extracts with lignocellulolytic activities capable of converting biomass into glucose monomers. The species *Panus lecomtei* displayed higher laccase and peroxidase activities, and co-cultivation with *Trichoderma reesei* increased laccase activities and the hydrolysis of pretreated sugarcane bagasse. In this study, it was also found that the OPDC composition induces greater enzyme release compared to MF. It is worth noting that the biomass employed in this study as a substrate for fungal growth of oil palm was used without previous treatment, only sterilization, with the addition of only supplements such as glucose, yeast extract, and minerals.

The majority of published studies on the degradation of lignocellulosic biomass from oil palm with mushrooms are focused on the either production of lignocellulolytic enzymes or the examination of their potential in biological pretreatment. However, there is potential in such an approach for the production of other enzymes of industrial interest, such as tannases and phytases, that can reduce tannins and phytates in plant material used for animal feed [114, 115]. The cost–benefit of using these enzymes in animal feed may also be improved when methods such as the cultivation of phytase/tannase-producer mushrooms are

**Table 3** (continued)

| Mushroom specie | Maximum enzyme production | Oil palm residue substrate | Type of culture | Ref |
|---|---|---|---|---|
| *P. lecomtei* | • Laccase (383.1 U.mL$^{-1}$), 7th day<br>• Peroxidase (341.4 U.mL$^{-1}$), 7th day<br>• Cellulase (FPase) (0.17 U.mL$^{-1}$), 7th day<br>• Xylanase (0.24 U.mL$^{-1}$), 7th day | OPDC | Submerged fermentation | [94] |
| | • Laccase (0.85 U.mL$^{-1}$), 7th day<br>• Peroxidase (99.39 U.mL$^{-1}$), 7th day<br>• Cellulase (FPase) (0.15 U.mL$^{-1}$), 7th day<br>• Xylanase (0.06 U.mL$^{-1}$), 7th day | MF | Submerged fermentation | |
| *T. versicolor* | • Laccase (270.4 U.mL$^{-1}$), 7th day<br>• Peroxidase (87.0 U.mL$^{-1}$), 7th day<br>• Cellulase (Fpase) (0.14 U.mL$^{-1}$), 7th day<br>• Xylanase (0.11 U.mL$^{-1}$), 7th day<br>• Betaglucosidase (0.23 U.mL$^{-1}$), 7th day | OPDC | Submerged fermentation | |
| | • Laccase (6.30 U.mL$^{-1}$), 7th day<br>• Peroxidase (7.65 U.mL$^{-1}$), 7th day<br>• Cellulase (Fpase) (0.15 U.mL$^{-1}$), 7th day<br>• Xylanase (0.07 U.mL$^{-1}$), 7th day | MF | Submerged fermentation | |
| *Coprinus* sp. | • Laccase (2.46 U.mL$^{-1}$), 7th day<br>• Peroxidase (5.74 U.mL$^{-1}$), 7th day<br>• Cellulase (Fpase) (0.42 U.mL$^{-1}$), 7th day<br>• Xylanase (0.50 U.mL$^{-1}$), 7th day<br>• Betaglucosidase (0.12 U.mL$^{-1}$), 7th day | OPDC | Submerged fermentation | |
| | • Cellulase (Fpase) (0.14 U.mL$^{-1}$), 7th day<br>•Xylanase (0.05 U.mL$^{-1}$), 7th day | MF | Submerged fermentation | |
| *P. lecomtei/T. reesei* (Coculture) | • Laccase (1111.4 U.mL$^{-1}$), 7th day<br>• Peroxidase (599.7 U.mL$^{-1}$), 7th day<br>• Cellulase (Fpase) (1.17 U.mL$^{-1}$), 7th day<br>• Xylanase (0.58 U.mL$^{-1}$) 7th day<br>• Betaglucosidase (0.19 U.mL$^{-1}$), 7th day | OPDC | Submerged fermentation | |
| *Pleurotus* sp. | • Laccase (18 U.mL$^{-1}$), 21st day<br>• Peroxidases ( 21 U.mL$^{-1}$), 7th day<br>• Lignin peroxidase (9 U.mL$^{-1}$), 6th day<br>• Manganese peroxidase(15 U.mL$^{-1}$), 13th day<br>• FPase (0.4 U.mL$^{-1}$), 21st day<br>• Xylanase (5 U.mL$^{-1}$), 13th day | EFB | Solid fermentation | [187] |

used instead of reliance on purchasing specific enzymes. Phytase activity has been detected in fruiting bodies and SMS of the commercial mushrooms *Agaricus bisporus*, *Lentinula edodes*, *Pleurotus cornocupiae*, and *Grifola frondosa* [116]. Tannases have also been isolated in the non-commercial white-rot fungi *Phellinus pili*, *Fomes fomentarius*, and *Tyromyces pubescens* [117], although this enzyme is typically obtained from cultivation of *Aspergillus* and *Penicillium* species [118, 119]. The highly toxic *Jatropha curcas* L. seed cake can be significantly detoxified by reducing phytate and tannin concentration after the cultivation of the edible mushroom *P. ostreatus*. This treatment has also been shown to decrease phorbol esters (99%) and enhance inorganic phosphorous and protein bioavailability, relevant concerning increasing digestibility of residual lignocellulosic materials [120].

## 5 Production of edible mushroom in oil palm residues

In addition to enzymes, mushrooms produce numerous biologically active substances, which can perform structural functions in the cell wall, such as polysaccharides (mainly β-glucans), proteins, and protein-carbohydrate complexes, or that are secreted as secondary metabolites, such as phenolic compounds, terpenoids, and steroids [121]. The medicinal properties of commercial edible mushroom species have been recently explored, indicating possible uses as antidiabetics, antioxidants, or antimicrobials, as well as antitumor, anti-inflammatory, or immunomodulating activities [121]. The presence of bioactive substances in mushrooms also increases the nutritional value to both humans and animals, taking into account that they also provide considerable levels of proteins (10–40%), essential amino acids (34–47%, including cysteine, threonine, valine, lysine, leucine, isoleucine, tryptophan, and methionine), vitamins (0.031–0.65%, including riboflavin, niacin, folates, vitamin C, D, and B complex), carbohydrates (35–70%, mainly oligosaccharides), and fatty acids (2–8%, mostly polyunsaturated fatty acids as oleic and linoleic acids) [121, 122].

Currently, the mushroom market is estimated at least US $ 35,000 million and is expected to continue growing to US$ 53,000 million by 2027 [123]. Per capita consumption per year has reached 4.7 kg (fresh weight), with China the country with the highest production, with 87% of the global total [124]. The greatest production is currently for the species *P. ostreatus*, *L. edodes*, *A. bisporus*, and *Auricularia* spp., which are typically cultivated on plant substrates, usually from agricultural residues.

In the case of oil palm lignocellulosic residues, there is as yet no established formula for mushroom cultivation for any of the various residue types that are generated in the field or the mills. Given the seven possible forms of lignocellulosic biomass generated in the oil palm industry, it is likely that each will affect cultivation, with the availability of nutrients potential limiting factor for the qualitative and quantitative yield of mushrooms (Fig. 4). Several experiments have shown that oil palm lignocellulosic residues can indeed increase the productivity of some species of mushrooms. In Triyono et al. [125], EFB was used as the main substrate for mushroom production of *V. volvacea*. Maximum mushroom productivity was 29.50 kg.tonne$^{-1}$, with 41.0% of protein content achieved when 1000 kg of EFB was supplemented with chicken manure (80 kg), rice bran (70 kg), and lime (60 kg). According to the authors, local farmers usually obtain up to 17 kg. tonne$^{-1}$ for the commercial cultivation of *V. volvaceae*. In a study to integrate bioconversion of EFB for the production of biogas with *V. volvacea* mushroom cultivation, maximum production of 47.30 kg.tonne$^{-1}$ of EFB and methane at 73.3 m$^{2}$.tonne$^{-1}$ of the spent mushroom substrate was achieved with POME [95], indicating feasibility in integrating various processes such as high-yield mushroom cultivation and other types of high-value-added products using oil palm biomass as raw material, as described in Fig. 4. In Marlina et al. [126], a study that also employed EFB as the main substrate, supplemented with rice bran, sawdust, calcium carbonate, and mineral fertilizer, a maximum *P. ostreatus* mushroom production of 459.5 kg per tonne$^{-1}$ of EFB supplemented with rice bran, $CaCO_3$, sawdust, and mineral fertilizer, was achieved after 124 days cultivation. It is important to mention that in this study, the control treatment without EFB did not result in the formation of fruiting bodies of *P. ostreatus*, highlighting the great potential of EFB for the cultivation of commercially important fungi.

In a study carried out to determine the social, economic, and environmental impact of the use of different types of lignocellulosic biomass from the oil palm industry [127], it was found that EFB used for the cultivation of mushrooms provides a Social Return of Investment (SROI) index of 2.35. This value is only minor when compared to using OPF as animal feed. The SROI index makes it possible to evaluate the benefits in social and environmental aspects in addition to the economic focus, which is important for an industry that has family farming in its structure and that at the same time has a strong negative environmental impact due to deforestation.

The use of lignocellulosic biomass from oil palm for mushroom cultivation has not been limited to EFB alone. In Saidu et al. [128], Mesocarp Fiber (MF) was used as the substrate for the production of *P. ostreatus.* It was demonstrated that a formulation composed of 100% MF does not have the nutritional requirements to sustain the production of *P. ostreatus* mushrooms, mainly due to the very high moisture retention capacity and oil residues present. As such, it is necessary to maintain a proportion between 50 and 80% of MF and supplement with other types of substrates such as rice bran, sawdust, and lime. In Silva et al. [129], the formulation (w/w) 84.6% Oil Palm Mesocarp Fiber (MF), 9.4% cocoa almond peels, 3% triturated charcoal, and 1% $CaCO_3$ was used to obtain a maximum *P. ostreatus* mushroom yield of 560.5 kg·tonne$^{1}$ and biological efficiency of 148.8% (mushroom fresh weight/substrate dry weight). Interestingly, the authors compared different proportions of MF and showed that the higher proportions (86.4, 76.8, and 67.2%) resulted in better mushroom production than the lower values (8.0%), indicating that increased proportions of MF in a formulation for the culture of *P. ostreatus* can lead to better results of biological efficiency and yield.

There are many opportunities to mix two types of plant biomass from oil palm in formulations for mushroom cultivation. In Wan et al. [130], *P. ostreatus* growth and yield were evaluated in a formulation with biochar obtained from vacuum microwave pyrolysis of KS and rice bran and sawdust. The addition of 2.5% (w.w$^{-1}$) biochar of KS in the substrate enabled maintenance of the percentage of humidity during cultivation (99%), and a neutral pH (6.8–7) of the medium, which contributed to mycelium growth and production of mushrooms with a maximum yield of 560 g.Kg$^{-1}$ (or 560 kg.tonne$^{-1}$) of substrate rice bran, sawdust, and KS biochar. It is interesting to note that the study compared results to those obtained following the addition of lime powder, a supplement used in mushroom cultivation to neutralize the culture media, which, when it was added at 2.5% in the substrate of rice bran and sawdust, presented a maximum yield of mushrooms of 600 g.Kg$^{-1}$ (or 600 kg.tonne$^{-1}$), a very similar yield value. This indicates that it is possible, through physicochemical treatments such as pyrolysis, to convert a plant residue that does not have ideal characteristics for the production of mushrooms into a substitute for supplements such as lime powder, and also can reduce heavy metals and other toxic components [131].

Although there is no fixed formulation for the various types of oil palm biomass in the production of mushrooms, it is understood that the composition of these formulations requires a specific C/N ratio, between 20/1 and 50/1 according to Elisa-Esposito [132]. Thus, at least with EFB, MF, and KS vegetable biomasses, there is an opportunity to integrate other agribusiness chains that also generate large amounts of plant residues as a strategy to establish more nutritious formulations for mushroom cultivation.

## 6 Spent mushroom substrate from oil palm residues as animal feed

The application of lignocellulosic biomass from oil palm to feed ruminants is not recent, especially for OPF [133, 134]. According to studies, producers affirm that the use of OPF as a constituent of animal feed generates a cost-saving effect, in addition to not affecting weight gain or the quality of animal meat. In addition, in terms of socio-economic and environmental impact, the use of OPF as animal feed presents a high SROI index of 5.47, according to Phoochinda [127]. However, here, we explore the potential of the different lignocellulosic biomasses of the oil palm industry for animal feed, following biological treatment by mushrooms (Fig. 4). SMS, rather than raw biomass, is advantageous because of the higher protein and nutraceutical content, as well as increases in digestibility for monogastric consumption.

SMS is a fermented soil-like material product after harvesting mushrooms and represents a potential source of animal feed. In addition to increasing digestibility after cell wall moieties degradation, in SMS the crude protein content is also increased, making it a useful source of nitrogen for various animal species [135]. Fazaeli et al. [136] used SMS of *A. bisporus* grown in wheat straw to feed calves. The addition of < 15% of SMS did not lead to significant differences in the carcass and internal organs of the calves that received this diet compared to controls. Furthermore, it has been shown that fungal fermentation processes also lead to the detoxification of molecules such as gossypol and phorbol esters, as was demonstrated through solid-state fermentation using the mushrooms *Fistulina hepatica*, *P. lecomtei*, and *P. pulmonarius* cultures in seed cakes of *Jatropha* seed and cotton, respectively [137, 138].

Mycelial residual in SMS retains similar bioactive properties to fruit bodies of mushrooms [139]. Strong antioxidant activity in vitro was detected in SMS of *P. eryngii*, related to the high concentration of crude and refined polysaccharide from liquid extracts obtained from this cultivation [140]. In ruminant feeding, the liquid extract obtained from SMS of *Ganoderma balabacense* had no negative effect on yield and quality of dairy cow's milk, nor on the biochemical index in blood compared to a basal medium composed mainly of corn. In addition, there was a reduction in the somatic cell count, possibly related to the antimicrobial bioactivity of polysaccharides of *Ganoderma*, indicating an immunomodulatory and antimicrobial property of the extract [141].

The positive effect of SMS in feeding has also been demonstrated in monogastric species, such as birds and fish. In Wang et al. [142], broiler chickens were fed on 10% SMS of *P. eryngii* cultured on wheat bran in solid-state fermentation, with no negative effect in growth performance, body weight, feed intake, and feed conversion compared with unfermented and control treatments. Molecular analysis revealed an increase in antioxidant regulator-Nfr2 expression in the chickens, a transcription factor of the cytoprotective antioxidant enzymes haem oxygenase-1 (HO-1) and glutathione s-transferase (GST). In SMS, high laccase, phytase, and manganese peroxidase activities were detected, associated with an increase in bioavailability of nutrients and an increase in flavonoids, phenolic compounds (gallic acid), and polysaccharide content, indicating that SMS of *P. eryngii* is highly suitable in poultry feeds. A positive effect on the growth performance of geese fed on SMS of *P. ostreatus* was also demonstrated [143]. It was shown that using 5% of *P. ostreatus* SMS as a component in feed for geese, no adverse effects on growth performance or meat characteristics were observed; blood biochemical analysis also showed higher antioxidant activities after 12 weeks of treatment. This condition also enhanced the sensory evaluation of geese meat flavor, juiciness, color, and acceptability. As the presence of high antioxidant elements in feed could reduce the cell damage of animals by protecting against free radicals, this is an important factor when choosing feed.

### 6.1 Fungal-treated plant-derived supplements for monogastric animal feed

Various concerns should be considered when employing plant-derived materials as supplements for monogastric animal feed. The first to consider is digestibility. This aspect implies not only considering the natural composition of feed, but also the absorption degree of nutrients and energy. In ruminants, absorption of nutrients from the plant cell wall is aided by a symbiont relationship with microorganisms that can degrade structural polysaccharides (hemicellulose and cellulose) using hydrolytic enzymes [144]. However, lignin concentration and composition (mainly syringyl-type) show a negative correlation with digestibility in the rumen, by shielding against the enzymatic hydrolysis of polysaccharides. On the other hand, in monogastric animals, the ruminant system is absent and there are specific adaptations to feed digestion.

The second concern is related to antinutrient factors present in plant-derived supplements. In general, these affect the assimilation of proteins, minerals, and vitamins, decrease growth performance, and also induce intoxication reactions. They include protease inhibitors, oligosaccharides, non-starch polysaccharides, cyanide, tannins, lectins, phytates, gossypol, oxalates, alkaloids, glucosinolates, antivitamins, saponins, and phorbol esters [145]. Antinutrient content differs according to plant origin and, in some cases, can be reduced in concentration by heating (e.g., protease inhibitors, lectins, tannins), alkali pretreatment (tannins, oligosaccharides, and non-starch polysaccharides), adding chelating substances, or using enzymes (phytates) [145]. However, this may consequently reduce the simplicity of using plant-derived material as animal feed.

Increasing the digestibility of lignocellulosic biomass for ruminants has been evaluated by using fungal pretreatment. Shrivastava et al. [146] demonstrated an increase in organic matter digestibility and crude protein content after solid-state fermentation of wheat straw with the white-rot fungi *P. ostreatus* and *T. versicolor*. Chen et al. [147] evaluated solid fermentation with *P. ostreatus* to reduce the lignin content in cornstalk and thus, increased the biodigestibility for animal feed. The data showed a reduction in acid-insoluble lignin and crystallinity (highest reduction with 7.6% and 15.2% after 30 days, respectively) and formation of cavities in the plant cell wall, indicating structural damage. Tao et al. [148] investigated co-cultures (a consortium of two or more species) of the white-rot fungus *Phanerochate chrysosporium* with *Aspergillus niger*/*Trichoderma viridae* cultivated in solid-state fermentation of maize stalk for development of feed for sheep. Results demonstrated that the co-culture of *P. chrysosporium*–*T. viridae* increased the ruminal degradability of dry matter, organic matter, neutral and acid detergent fiber, acid detergent lignin, and cellulose.

Fungal pretreatment of plant biomass by white-rot fungi breaks linkages between lignin and cellulose or hemicellulose, making fiber fractions more easily accessible for utilizing and also for the breakdown of peptide bonds of fiber-bound protein [149]. Aldoori et al. [150] evaluated the effect of dietary replacement of barley with SMS of *P. ostreatus* on Awassi lambs, demonstrating that 15% of SMS could be included without any negative effect on carcass characteristics. Improving the nutritional quality of cocoa pods (*Theobroma cacao*) for lamb feed has also been investigated through different treatments, including colonization with *P. chrysosporium*. The spent mushroom substrate from *P. chrysosporium* improved the in vitro dry matter and organic matter digestibility of this material to levels similar to those achieved using urea treatment. In addition, this method increased crude protein content, attributed to the mycelial growth [151].

Monogastric species have been the focus in feed development with SMS as they cannot degrade cellulose as efficiently as ruminants. Broiler chicken production was evaluated after including SMS from *P. ostreatus* in the diet. The replacement of standard diet by colonized substrate resulted in body weight gain and no meat taste alteration. This approach also increased the hematocrit, heterophils, typical lymphocyte, total cholesterol, high-density lipoproteins, and decreased low-density lipoproteins [152]. The mushroom-supplemented feed can modify the intestinal microbiota composition in birds and consequently improve gastrointestinal function, digestibility, and performance. Certain mushroom polysaccharides are hydrolyzed and fermented at the intestinal level, producing straight-chain fatty acids (SCFA) and net utilization of ammonia for the growth of bacteria, which is beneficial for health. Additionally, these polysaccharides also provide bioactive properties in monogastric animals, mainly due to their sugar composition, molecular weight, and structure [153, 154].

### 6.2 Oil palm residues fermented by fungi for fish feed

Currently, the main food sources for fish feed in aquaculture are fish meal and fish oil. Plant-derived supplements, however, appear to offer an excellent opportunity in fish feed development. Among plant-derived supplements, the most prominent example is soybean meal, given the high content of protein and carbohydrates, balanced amino acid profiles, global availability, and lower prices compared to the fish meal [155, 156]. Recently, soybean meal has shown promise as a feed supplementation in marine and carnivorous fish species such as black sea bream (*Acanthopagrus schlegeli*), turbot (*Scophthalmus maximus*), and tench (*Tinca tinca*), where a suitable percentage of fish meal replacement is around 25–40% [157, 158]. Other relevant crop products include barley, canola protein concentrate, corn gluten protein, wheat gluten protein, and cottonseed meal that have been proposed as feed supplements [159].

Studies related to the use of oil palm by-products as fish feed are limited. Reports of this material in animal feed after biological pretreatment by microorganisms are also scarce, possibly because priority is given to other types of plant residues with better geographical availability and quantities. In Lim et al. [160], OPKC was employed as a feed of *Oreochromis mossambicus* after solid-state fermentation with the fungus *Aspergillus flavus*. OPKC could partially substitute other protein feeds as high as 30% without any adverse effect on fish growth and feed utilization efficiency. Ng [161] also used OPKC in the *Oreochromis* sp. diet after solid-state fermentation by *Trichoderma koningii* or enzymatic digestion, showing that OPKC could be included in the diet as high as 20% using both fermented and enzymatic treated biomass, without affecting the growth performance of fish. The same author demonstrated that including up to 20% of OPKC in the *Clarias macrocephalus* × *C. gariepinus* diet could show similar results [162]. These investigations exemplified the potential use of fungal species to enhance the nutritive value of lignocellulosic biomass.

### 6.3 Oil palm residues fermented by fungi for poultry feed

In Malaysia and Indonesia, where oil palm production is high, oil palm kernel has been used as a supplement in a compound feed of ruminants, mainly due to its crude protein content ≥ 15% [163]. Nevertheless, the use in feed for monogastric is very limited, given the high fiber content and low metabolizable energy [164]. Poultry shows a low digestive enzymatic activity to process the non-starch polysaccharide (NSPs) of the cell wall of PKC, and some components such as arabinoxylans, pectins, and β-glucans of NSPs create a viscous environment in the gastrointestinal tract that has negative effects on nutrient utilization, especially in younger birds [165].

To improve the nutritional value of OPKC, physical or chemical treatment can be performed to reduce the fiber content [163]. However, studies related to the improvement of OPKC for poultry feed used enzymes as catalytic agents, especially carbohydrate-degrading and proteolytic enzymes, or through the fermentation process using microorganisms. Pasaribu et al. [166] evaluated OPKC fermentation using a microbial cocktail of *Bacillus amyloliquefacien* and *Trichoderma harzianum*. The results showed a 2.3% reduction in crude fiber, related to the activity of endo-β-glucanase, (CMCase), and β-glucanase enzymes. The treatment also increased the protein content by 24–32% and the amino acids glutamate, arginine, and methionine compared with the untreated OPKC, indicating that fermented OPKC by microbial cocktails is suitable for use as poultry feed. A previous study demonstrated that solid-state fermentation of OPKC by *A. niger* can completely substitute the soybean meal protein, with no negative significant effect on feed consumption, body weight, feed conversion, or percentage of carcass [167]. Recently, OPKC was also evaluated as a suitable feed compound after fermentation using *A. niger*, *Trichoderma viride*, or *P. ostreatus* [168]. A positive effect on the nutrition of broilers was shown in the treatments, with 10% and 20% fungi fermented OPKC, but especially in the 20% treated with *A. niger*, which resulted in higher body weight in broilers than observed in control basal diets.

## 7 Knowledge gaps and perspectives

The use of lignocellulosic biomass generated from the oil palm industry has shown a wide range of applications for biotechnological processes (Table 2). This potential has an important commercial component since it allows obtaining bioenergy in the form of biofuels or different types of low-cost biomaterials because this type of raw material is low-cost and it is characterized by its high availability [169]. One of the main opportunities of oil palm lignocellulose biomass is as a substrate for the growth of edible mushroom-forming fungi, from which high value-added products can be obtained. However, the feasibility of integrating industry and biotechnology supported by techno-economic studies has not yet been widely discussed.

During fungal growth, lignocellulose is converted into more digestible fragments for animal consumption, rich in bioactive compounds. This bioconversion is carried out by the secretion of enzymes whose catalysis allows the obtaining of sugars, and at the same time it is possible to recover these lignocellulolytic or proteolytic enzymes with great commercial potential. The main advantage of bioconversion mediated by microorganisms such as fungi, in contrast to chemical or physical pretreatments, is that it does not require sophisticated equipment, large energy investment, or the need to clean chemical effluents that inhibit saccharification or fermentation, which means high application costs [170]. However, the growth dynamics of microorganisms are limited by time and specific conditions such as humidity, temperature, and sterility, which are an obstacle to scale-up from laboratory to industrial level. New strategies have been proposed to overcome these obstacles. Strategies such as the elimination of the sterilization step and the reduction of the culture time were evaluated to improve the conditions of the processes and reduce the effects of bottlenecks from biological pretreatment on an economic level [169].

In biological pretreatment, it is possible to obtain edible mushrooms, and this may be another important economic opportunity in a scenario where oil palm biomass is used as a substrate. Comparison of various technologies and types of oil palm biomasses regarding benefits, costs, and risks for smallholders in rural areas of Riau province (Indonesia) have shown the main opportunities of using EFB in mushroom production relies on the fact that the food market is operationally easy and there is high availability of raw material (4.42 ton/ha/year)[171]. In addition, the environmental risks or failures in processes and markets are low, the revenue is high, and the labor is relatively low compared to other strategies, such as the use of the EFB for the manufacture of charcoal briquettes. However, studies in different regions and scales are still necessary to further support and expand these findings.

Enzymes such as cellulases are important in obtaining ethanol since they represent 43.5% of production costs [172]. Obtaining enzymes using the fungal pretreatment of oil palm biomass has been the subject of various application studies; however, the techno-economic bases of possible scenarios at small- or industrial-scale production have not yet been elucidated. In addition, the evaluation of costs in specialized equipment that provides the specific conditions for the growth and production of enzymes is an essential subject of research.

## 8 Conclusions

Given the high demand for palm oil across different markets and the large potential for expansion of cultivation in regions such as Brazil and Indonesia, increased efficiency of the production chain and development of appropriate biorefinery schemes with regard to oil palm plant residues are priorities. This latter focus is essential, considering that oils produced by pressing of mesocarp and fruit nuts represent only 10% of the plant biomass generated in the field. The rest of the biomass, if dispensed in fields, results in additional negative environmental impacts to those resulting from the deforestation conducted by this industry.

The implementation of renewable processes in an oil palm biorefinery scheme is still at the research and development phase. To reach viable industrial processes and applications, diverse biotechnology strategies have been evaluated by different groups around the world for the generation of products with high added value from the various types of lignocellulosic biomass residues obtained from this palm species. As lignocellulosic biomass is composed mainly of carbohydrates, most studies have focused on obtaining simple sugars through physicochemical pretreatments and hydrolysis for later use in fermentative processes. In addition, the application of pyrolysis and other techniques for bio-oils and gases has been increasing in recent years. The use of thermal techniques facilitates the conversion of different residues. Finally, the application of lignocellulosic residues from the palm oil industry in animal feed has gained attention recently. Here, the main challenge is to reduce recalcitrance and increase digestibility for certain species of farm animals. The enzymatic potential of specific fungi grown on these materials has now enabled the development of formulations without negative effects on animal performance.

The employment of lignocellulosic biomass from the oil palm industry for mushroom cultivation still requires further exploration to enable products with greater added value. Empty Fruit Bunches, Mesocarp Fibers, and Oil Palm Fronds are residues with the greatest number of studies conducted with regard to mushroom cultivation, mainly with regard to biological pretreatment, the production of ligninolytic enzymes such as laccases (which are important in the food industries, in detergent production, in bioenergy, and bioremediation), and as formulations of substrates for the production of edible fungi with significant yields and biological efficiency values. In terms of animal feed production, data is more limited, although promising results indicate that the oil palm industry and fungi culture have great potential within a biorefinery scheme.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

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