Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in
Green and Sustainable Chemistry

Recent advances in production of lignocellulolytic enzymes by solid-state fermentation of agro-industrial wastes

Paulina Leite[1], Daniel Sousa[1], Helena Fernandes[2,3], Marta Ferreira[1], Ana Rita Costa[1], Diogo Filipe[2,3], Margarida Gonçalves[1,2], Helena Peres[2,3], Isabel Belo[1] and José Manuel Salgado[1,2]

Agricultural, forestry, and food industries produce large amounts of lignocellulosic wastes every year. Land disposal of these residues without proper treatment leads to environmental pollution and negative health effects. The recent advances in valorization of agro-industrial wastes by the production of lignocellulolytic enzymes under solid-state fermentation (SSF) are reviewed. SSF is a promising technology to produce lignocellulolytic enzymes. However, the large-scale feasibility is the main challenge of SSF being the control of operational parameters and adequate reactor design the first locks. The current and future trends of SSF bioreactors for lignocellulolytic enzyme production are summarized. SSF allows the production of lignocellulolytic enzymes with high stability at different temperatures and pH, improving their applicability in different industrial settings.

Addresses
[1] Centre of Biological Engineering, University of Minho, Campus de Gualtar, 4710–057, Braga, Portugal
[2] Interdisciplinary Centre of Marine and Environmental Research (CIIMAR), Terminal de Cruzeiros do Porto de Leixões, Av. General Norton de Matos, 4450-208, Matosinhos, Portugal
[3] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Rua do Campo Alegre Ed. FC4, 4169-007, Porto, Portugal

Corresponding author: Salgado, José Manuel (jmsalgado@ceb.uminho.pt)

Current Opinion in Green and Sustainable Chemistry 2021, **27:**100407

This review comes from a themed issue on **Sustainable Solutions for Renewable Wastes**

Edited by **Sara González García** and **Beatriz Gullón**

https://doi.org/10.1016/j.cogsc.2020.100407

Introduction

Agricultural and food industrial activities generate large volumes of residues every year [1]. The sectors of agriculture, forestry, and fishing produced close to 21 million tons of wastes in the European Union during 2018 [2]. Nonetheless, higher waste production is expected in the next decades owing to the growth of the world population and the subsequent increase in food production [3].

The disposal of these materials is highly important and, when performed inadequately, may lead to environmental impacts [1]. Thus, waste management legislation became more restrictive in recent years. The European Commission's Circular Economy Action Plan comprises several actions to promote resource efficiency, moving toward a more sustainable world with less waste production (European Commission, 2019) [4].

However, the strategies currently used concerning agro-industrial wastes still hold some drawbacks. While unplanned landfilling and burning of wastes for energy purposes result in a negative environmental impact [5], their utilization as animal feed is impaired by low digestibility and the presence of antinutritional factors [6]. As per Directive 2008/98/EC of the European Parliament, agro-industrial wastes can be considered as by-products, when they can be used directly in other processes without any further processing, and further use is certain and lawful without adverse environmental or human health impacts.

Biotechnology can be a suitable tool to transform the agro-industrial wastes and by-products into raw materials to produce value-added products. In this sense, solid-state fermentation (SSF) is a biotechnology process with low environmental impact and low cost that can use directly agro-industrial by-products without pretreatments [7]. Most of these wastes and by-products are of lignocellulosic nature, which can favor the growth of microorganisms to produce lignocellulolytic enzymes [8]. The world market of enzymes could reach $7.0 billion in 2023 [9]. Lignocellulolytic enzymes represent more than 20% of worldwide sales of commercially available enzymes [10] and have applications in textile, food, animal feed, paper, biofuel, and pharmaceutical industries [9]. Table 1 shows the advantages and disadvantages of SSF compared with submerged fermentation. The industrial production of enzymes was focused on submerged fermentation

Table 1

Advantages and disadvantages of SSF compared with submerged fermentation.

Advantages	Disadvantages
Cost-effective	Engineering problems by increase of temperature, oxygen, heat, and mass transfer; pH control; substrate and moisture gradients; nonuniformity of the cell mass; temperature; pH; nutrients; moisture content
Eco-friendly	
Less energy	
Higher yield of enzymes	
Produces less wastewater with less risk of bacterial contamination	Steady aeration is difficult.
The process is less prone to problems with substrate inhibition.	Biomass measurement for microbial growth
The fermentation time may be shorter.	Growth and kinetics study is still difficult.
The degradation of enzymes by undesirable proteases is minimized.	

SSF, solid-state fermentation.
[12,55].

because it is easier to control the process and there are more industrial bioreactors. Despite the fact that SSF is often a longer process, the production of enzymes is higher, so that it has higher productivities than submerged fermentation. In addition, sometimes, the cultivation time of SSF of agro-industrial wastes for enzyme production can be shorter than submerged fermentation [11]. The lower water activity of solid substrate limits the growth of many microorganisms; thus, the sterilization step can be avoided, reducing the cost of process [7]. Other advantage of SSF is that the higher concentration of enzymes in SSF favored the downstream processing with respect to submerged fermentation [12].

The aim of this article is to review the recent advances in SSF of agro-industrial wastes and by-products as a sustainable solution to produce lignocellulolytic enzymes, focusing on SSF bioreactors.

Agro-industrial wastes with potential to be used in SSF for lignocellulolytic enzymes

Agro-industrial wastes are nutritionally rich, presenting high amounts of proteins, sugars, and minerals, combining the perfect environment for microbial growth [13]. SSF is a fermentative process that uses solids as a substrate for the growth of microorganisms and occurs in the absence or near absence of free water. However, the solid substrate must contain enough water to support the growth and metabolism of microorganisms [14]. This biotechnological process can use agro-industrial wastes as a substrate, which simultaneously serve as a support and source of nutrients for microbial growth, filamentous fungi being the best adapted to these conditions [7].

Recent studies reported the use of a wide range of organic residues as cheap substrates in SSF including rice bran, wheat bran, grape pomace, brewer's spent grain, oilseed cakes, coffee husk, wood chips, and olive pomace [15–20]. In fact, the vast majority of agro-industrial wastes used in SSF studies are lignocellulosic materials. The choice of an appropriate substrate influences the successful production of enzymes. As a matter of fact, lignocellulosic fractions are quite important once they can act as inductors or inhibitors for the production of ligninolytic enzymes [21]. The concentration of each lignocellulosic fraction affects the production of lignocellulolytic enzymes. Taherzadeh et al. [22] considered wheat bran as a proper source of carbon for the production of cellulases owing to the presence of low amounts of lignin and high levels of cellulose and hemicellulose. Tani et al. [23] reported the positive effect of cellulose in the production of cellulases and hemicellulases. In addition, Mejias et al. [21] reported lower cellulase production when the cellulose content of substrates is lower than 30%. Recently, advances in genome sequencing of a microorganism producer of lignocellulolytic enzymes have been explored; the genes of *Bacillus velezensis* linked to the degradation of xylan, cellulose, and lignin were identified [24], and they were related to the induction effect of xylan and cellulose content in the substrate.

Among the by-products explored, wheat bran is the most effective for xylanase and cellulase production by SSF; thus, it is used as a cosubstrate with other agro-industrial wastes [25]. Orange pomace is the main by-product used for pectinase production owing to the high content of pectin, which acts as an inductor [26,27]. The mixture of agro-industrial wastes is a strategy widely used to carry out SSF [15,28,29] because a single by-product may not provide all the essential nutrients for microbial growth.

The use of lignocellulosic wastes as substrates offers the possibility to reduce the production costs of lignocellulolytic enzymes because the costs of raw materials represent the third part of enzyme production costs [30]. Thus, the choice of a solid substrate plays an important role in the economic feasibility of enzyme production.

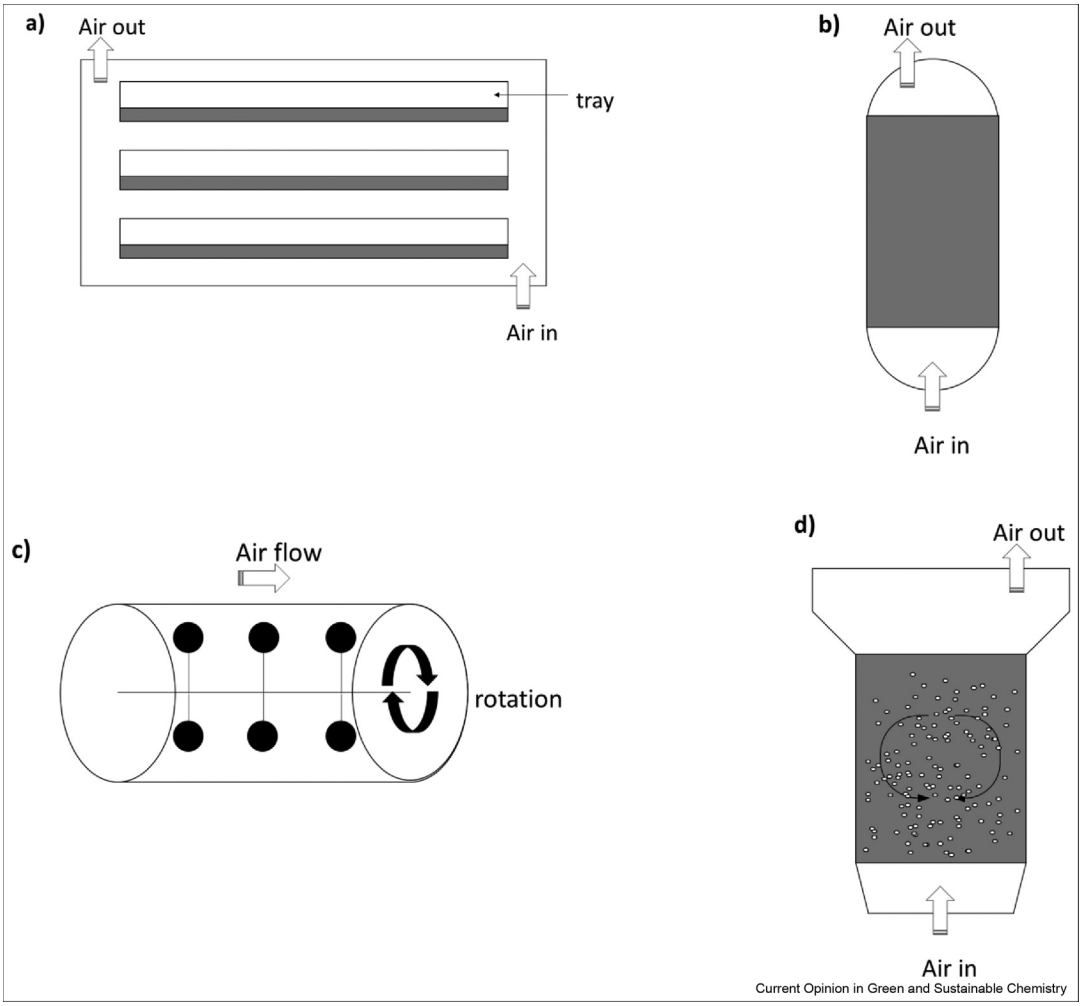
Production of lignocellulosic enzymes in SSF bioreactors

The great challenge of SSF is the scale-up of the process, and many studies on this topic have been reported recently. The use of SSF bioreactors to ferment agro-industrial wastes is mainly focused on cellulase, xylanase, and pectinase production.

Despite SSF process offering several advantages, fully developed bioreactors with a simple design and automatic process control are almost inexistent on the market [31]. The main problems of scaling up the production of enzymes by SSF are related to temperature, pH, moisture, and oxygen gradients inside of the bioreactor [32], which are due to the difficult agitation of the solid substrate. The bioreactors for SSF are designed to overcome these problems. They can be divided into four categories (Figure 1), based on the mode of operation: tray bioreactor, packed-bed bioreactor, fluidized bed bioreactor, and rotary drum bioreactor [33]. Tray bioreactors have a bed that remains almost static, and the air is circulated around it, not being forced to flow through. In packed-bed bioreactors, the bed remains static or is mixed infrequently with the air being blown forcefully into the bed, having to flow through the bed to get out. Differently, in the fluidized-bed bioreactor, the bed is agitated continuously, with air being blown forcefully into the bed, having to flow through the bed to get out. Finally, in the rotary drum bioreactor, the bed is constantly agitated in a horizontal drum, with the air being circulated through the headspace above the bed, not being forced to flow through the bed itself [34].

Table 2 shows recent studies of lignocellulolytic enzyme production using SSF bioreactors. Traditional bioreactors such as the tray type and packed-bed type continue to be the most used. The main advantage of the tray type is that the results easily scaled up, thus being reproducible at an industrial scale, because the

Figure 1



Bioreactors for SSF. **(a)** Tray; **(b)** packed-bed, **(c)** rotary drum, **(d)** fluidized bed bioreactor. SSF, solid-state fermentation.

Table 2

Recent studies (2017–2020) on SSF bioreactors used for enzyme production.

Enzyme	Microorganism	Substrate	Length of the SSF	Enzyme productivity	Bioreactor/solid (g)	Reference
Cellulase	*Myceliophthora thermophile*	Sugarcane bagasse and wheat bran	4 days	18.75 U g^{-1} d^{-1}	Packed bed/620 g	[25]
	Aspergillus ibericus	Winery and olive mill waste	14 days	4.0 U g^{-1} d^{-1}	Tray/400 g	[15]
	Trichoderma asperellum	Mixture of vine shoots, jatropha cake, olive pomace, olive oil	7 days	2.77 U g^{-1} d^{-1}	Packed bed/40 g	[29]
Xylanase	*Aspergillus niger*	Wheat bran	3 days	973 U g^{-1} d^{-1}	Tray/100 g	[56]
	M. thermophile	Sugarcane bagasse and wheat bran	4 days	100 U g^{-1} d^{-1}	Packed bed/620 g	[25]
	Aspergillus ibericus	Winery and olive mill waste	14 days	13.5 U g^{-1} d^{-1}	Tray/400 g	[15]
β-glucosidase	*Aspergillus ibericus*	Winery and olive mill waste	14 days	0.8 U g^{-1} d^{-1}	Tray/400 g	[15]
	Aspergillus niger	Coffee industry waste	5 days	8.72 U g^{-1} d^{-1}	Packed bed	[57]
β-mannanase	*Aspergillus niger*	Coffee industry waste	5 days	12.7 U g^{-1} d^{-1}	Packed bed	[57]
Pectinase	*Aspergillus niger*	Wheat bran and sugarcane bagasse	1 day	22 U g^{-1} d^{-1}	Packed bed/30 kg	[26]
	Aspergillus niger	Wheat bran, citric pectin, glucose, and salt solution	4 days	44.6 U g^{-1} d^{-1}	Rotating drum/2.5 kg	[28]
	Aspergillus niger	Orange pomace and sugarcane bagasse	4 days	17.5 U g^{-1} d^{-1}	Tray/285 g	[27]
	Aspergillus niger	Orange pomace	4 days	11.3 U g^{-1} d^{-1}	Rotating drum/285 g	
Polygalacturonase	*Aspergillus niger*	Cashew apple	77 h	2.15 U g^{-1} d^{-1}	Tray/500 g	[58]
Laccases	*Trametes versicolor*	Corn stalk	13 days	0.53 U g^{-1} d^{-1}	Tray	[39]
	Coriolus versicolor	Sweet sorghum bagasse	20 days	11.1 U g^{-1} d^{-1}	Tray/25 g	[38]
Lignin peroxidase	*Coriolus versicolor*	Sweet sorghum bagasse	20 days	0.26 U g^{-1} d^{-1}	Tray/25 g	[38]
Mn peroxidase	*Coriolus versicolor*	Sweet sorghum bagasse	20 days	1.4 U g^{-1} d^{-1}	Tray/25 g	[38]

SSF, solid-state fermentation.

height of the bed can be maintained, only varying the number of trays [7]. On the other hand, the performance of packed-bed bioreactors is affected by scaling up from the bench to pilot scale, mainly owing to limitations of heat transfer and air diffusion [25].

As depicted in Table 2, most of the works reporting on enzyme production by SSF of agro-industrial wastes are focused on cellulases, xylanases, and pectinases, but other enzymes such as laccases and peroxidases have also been pursued.

Trichoderma reesei and *Aspergillus niger* are the most important industrial producer of lignocellulolytic enzymes [35]. Other microorganisms are also being studied in the last years, as can be seen in Table 2. An interesting alternative is the use of the thermophilic fungus for enzyme production [25]. These strains can produce enzymes with higher thermostability that present important advantages for several industrial settings [36].

The great challenge for lignocellulosic waste valorization into value-added products is delignification [37]. Lignocellulolytic enzymes linked to the degradation of lignin are the laccases, lignin peroxidases, and Mn peroxidases. Lignin acts as a rigid barrier, which hinders the access of enzymes to cellulose [38]. White-rot fungi can grow on lignocellulosic materials and to produce peroxidases for degradation of the lignin fraction [39], improving the subsequent enzymatic hydrolysis of cellulose fraction. However, the production of ligninolytic enzymes in bioreactors was hardly studied, focusing on the use of tray-type bioreactors.

Application of lignocellulosic enzymes produced by SSF

Lignocellulolytic enzymes such as xylanases, cellulases, laccases, and lignin peroxidases obtained in SSF by fungi or bacteria are used in several industries owing to their ability to hydrolyze fibers and release polyphenolic compounds. The enzymes are extracted from the fermented solid by *in situ* recovery of aqueous solutions in SSF bioreactors or other bioreactors. The downstream process consists of the obtention of crude extract with a filtration step to remove the fermented solid, ultrafiltration to remove the microorganism, and concentration of the product and lyophilization to obtain the enzyme as a dry solid [40].

The enzymes produced by SSF show generally higher stability than the ones produced by submerged fermentation at different temperatures and pH [41]. The thermostability and resistance to alkaline or acidic conditions are important for the application of enzymes in the industrial processes [42].

Lignocellulolytic enzymes can enhance the nutritional value of feed ingredients with a high amount of fiber because they can aid in the disruption of the lignocellulosic structure by degrading β-1,4 bonds in cellulose [43]. Different studies have observed an improvement in feed utilization and growth performance of ruminants, broilers, and pigs [44,45].

In food industry, polygalacturonase, cellulases, and xylanases are frequently used in juice, beer, and wine industries owing to their ability to clarify juices obtained from fruits and vegetables, turbidity of which is caused by floating cellulosic materials [46–48]. They also decrease the viscosity of juices, beer, and wine, facilitating the filtration of these products and improving the yield of these beverages [49]. Laccases can be used for stabilization of wine beer and juice [50]. Lignin peroxidases are used in the production of natural aromatic compounds through lignin degradation [51].

Lignocellulosic enzymes can be used to produce second-generation biofuels by hydrolyzing hemicellulose and cellulose to simple sugars and, subsequently, using these sugars to obtain ethanol [52]. The optimal conditions of enzymatic hydrolysis and the pretreatment of biomass should be studied to achieve 100% yields of glucose and xylose [52].

Lignocellulolytic enzymes can be used in textile industries for various purposes [53]. In pulp and paper industries, a mixture of several enzymes obtained from SSF can be used for biopulping of lignocellulosic materials to produce paper [54].

Future challenges and conclusions

As a consequence of the fast increase of the global population, one of the major challenges humanity faces today is the increase in generation of solid waste. Thus, new strategies to reuse wastes and obtain value-added products are mandatory to relieve pressure on natural resources. Correct reutilization of wastes and by-products, using green technologies, helps to mitigate the negative and harmful effects of waste disposal and produce value-added compounds, contributing to the implementation of the circular economy. The cascade utilization of agro-industrial wastes is a challenge for their valorization at the industrial scale. SSF can be a suitable technology to achieve it.

SSF is a low-cost biotechnological process that has gained attention over the past years for the production of lignocellulolytic enzymes from agro-industrial wastes. The production of these enzymes at the pilot scale is carried out using the tray-type and packed-bed bioreactor. However, these systems show limitation in fermenting large quantities. Future advances in the design of bioreactors are needed to improve the scale-up of production of lignocellulolytic enzymes by SSF. Bioreactors continuously fed with agro-industrial biomass can be a solution to bioprocess large quantities of wastes and increase the production of lignocellulolytic enzymes. On the other hand, the use of the thermophilic fungus will allow production of more stable enzymes, improving the application of enzymes in the industries.

This review mainly described the current situation of production of lignocellulolytic enzymes by SSF, which offers a clean alternative to close the loop on lignocellulosic residues and offers the possibility to obtain value-added products with several industrial applications. Thus, more advances in this field will have strong repercussions in the economy and environment.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the project 'Development of innovative sustainable protein and omega-3 rich feedstuffs for aquafeeds, from local agro-industrial by-products,' reference POCI-01-0145-FEDER-030377, funded by European Regional Development Fund (ERDF). JMS was supported by contract from this project. This study was supported by the Portuguese Foundation for Science and Technology (FCT) under the scope of the strategic funding of UID/BIO/04469/2019 unit and BioTecNorte operation (NORTE-01-0145-FEDER-000004) funded by the European Regional Development Fund under the scope of Norte2020 - Programa Operacional Regional do Norte. PL was supported by the PhD grant (SFRH/BD/114777/2016) funded by FCT. DS was supported by the doctoral programme 'Agricultural Production Chains – from fork to farm' (PD/00122/2012). HF was supported by the PhD grant SFRH/BD/131219/2017, and MF was funded by SFRH/BD/143614/2019, both funded by FCT. MG and DF were supported by project InovFeed (ref. MAR-02.01.01-FEAMP-0111; Mar2020).

References

Papers of particular interest, published within the period of review, have been highlighted as:

* of special interest
** of outstanding interest

1. * Nayak A, Bhushan B: **An overview of the recent trends on the waste valorization techniques for food wastes**. *J Environ Manag* 2019, **233**:352–370. https://doi.org/10.1016/j.jenvman.2018.12.041.
is a review of latest individual valorization technologies aimed at the generation of value-added by-products from food wastes in the form of bio-fuels, bio-materials, value added components and bio-based adsorbents.

2. Eurostat: *Generation of waste by economic activity*. 2016.

3. FAO: *The future of food and agriculture – alternative pathways to 2050, Rome*. 2018.

4. EuropeanComission: *European commission - implementation of the circular economy action plan*. 2019.

5. Sadh PK, Duhan S, Duhan JS: **Agro-industrial wastes and their utilization using solid state fermentation: a review**. *Bioresour. Bioprocess.* 2018, **5**:15. https://doi.org/10.1186/s40643-017-0187-z.

6. Tripathi MK, Mishra AS: **Glucosinolates in animal nutrition: a review**. *Anim Feed Sci Technol* 2007, **132**:1–27. https://doi.org/10.1016/j.anifeedsci.2006.03.003.

7. Soccol CR, da Costa ESF, Letti LAJ, Karp SG, Woiciechowski AL, Vandenberghe LP de S: **Recent developments and innovations in solid state fermentation**. *Biotechnol. Res. Innov.* 2017, **1**: 52–71. https://doi.org/10.1016/j.biori.2017.01.002.

8. * * Leite P, Silva C, Salgado JM, Belo I: **Simultaneous production of lignocellulolytic enzymes and extraction of antioxidant compounds by solid-state fermentation of agro-industrial wastes**. *Ind Crop Prod* 2019, **137**:315–322. https://doi.org/10.1016/j.indcrop.2019.04.044.
in this work was evaluated the increase of antioxidant compounds extraction from agro-industrial wastes after SSF and to relate it to the production of lignocellulolytic enzymes.

9. * * Saldarriaga-Hernández S, Velasco-Ayala C, Leal-Isla Flores P, de Jesús Rostro-Alanis M, Parra-Saldivar R, Iqbal HMN, Carrillo-Nieves D: **Biotransformation of lignocellulosic biomass into industrially relevant products with the aid of fungi-derived lignocellulolytic enzymes**. *Int J Biol Macromol* 2020, **161**: 1099–1116. https://doi.org/10.1016/j.ijbiomac.2020.06.047.
is a review that described the role of lignocellulolytic enzymes in the biotransformation of lignocellulosic biomass into value-added products. The review described the potential and current industrial applications of the involved fungal enzymes.

10. Toushik SH, Lee KT, Lee JS, Kim KS: **Functional applications of lignocellulolytic enzymes in the fruit and vegetable processing industries**. *J Food Sci* 2017, **82**:585–593. https://doi.org/10.1111/1750-3841.13636.

11. Hölker U, Höfer M, Lenz J: **Biotechnological advantages of laboratory-scale solid-state fermentation with fungi**. *Appl Microbiol Biotechnol* 2004, **64**:175–186. https://doi.org/10.1007/s00253-003-1504-3.

12. Webb C: **Design aspects of solid state fermentation as applied to microbial bioprocessing**. *J. Appl. Biotechnol. Bioeng.* 2017, **4**: 511–532. https://doi.org/10.15406/jabb.2017.04.00094.

13. Rouilly A, Rigal L: **Agro-materials: a bibliographic review**. *J Macromol Sci Polym Rev* 2002, **42**:441–479.

14. Pandey A: **Solid-state fermentation**. *Biochem Eng J* 2003, **13**: 81–84. https://doi.org/10.1016/S1369-703X(02)00121-3.

15. Filipe D, Fernandes H, Castro C, Peres H, Oliva-Teles A, Belo I, Salgado JM: **Improved lignocellulolytic enzyme production and antioxidant extraction using solid-state fermentation of olive pomace mixed with winery waste**. *Biofuels, Bioprod. Biorefining.* 2019, **14**:78–91. https://doi.org/10.1002/bbb.2073.

16. Janarny G, Gunathilake K: **Changes in rice bran bioactives, their bioactivity, bioaccessibility and bioavailability with solid-state fermentation by Rhizopus oryzae**. *Biocatal. Agric. Biotechnol.* 2020, **23**:101510.

17. Tu J, Zhao J, Liu G, Tang C, Han Y, Cao X, Jia J, Ji G, Xiao H: **Solid state fermentation by Fomitopsis pinicola improves physicochemical and functional properties of wheat bran and the bran-containing products**. *Food Chem* 2020:127046.

18. Sousa D, Venâncio A, Belo I, Salgado JM: **Mediterranean agro-industrial wastes as valuable substrates for lignocellulolytic enzymes and protein production by solid-state fermentation**. *J Sci Food Agric* 2018, **98**:5248–5256.

19. Lee JH, Hwang CE, Son KS, Cho KM: **Comparisons of nutritional constituents in soybeans during solid state fermentation times and screening for their glucosidase enzymes and antioxidant properties**. *Food Chem* 2019, **272**:362–371.

20. * Marín M, Artola A, Sánchez A: **Optimization of down-stream for cellulases produced under solid-state fermentation of coffee husk**. *Waste and Biomass Valorization* 2019, **10**:2761–2772.
in this work was studied the downstream process of the solid state fermentation (SSF) of a mixture of coffee husk and wood chips for cellulase production.

21. Mejias L, Cerda A, Barrena R, Gea T, Sánchez A: **Microbial strategies for cellulase and xylanase production through solid-state fermentation of digestate from biowaste**. *Sustainability* 2018, **10**:2433.

22. Taherzadeh-Ghahfarokhi M, Panahi R, Mokhtarani B: **Optimizing the combination of conventional carbonaceous additives of culture media to produce lignocellulose-degrading enzymes by Trichoderma reesei in solid state fermentation of agricultural residues**. *Renew Energy* 2019, **131**:946–955.

23. Tani S, Kanamasa S, Sumitani J, Arai M, Kawaguchi T: **XlnR-independent signaling pathway regulates both cellulase and xylanase genes in response to cellobiose in Aspergillus aculeatus**. *Curr Genet* 2012, **58**:93–104. https://doi.org/10.1007/s00294-012-0367-5.

24. * * yu Zhang Z, Raza MF, Zheng Z, Zhang X, Dong X, Zhang H: **Complete genome sequence of Bacillus velezensis ZY-1-1 reveals the genetic basis for its hemicellulosic/cellulosic substrate-inducible xylanase and cellulase activities**. *3 Biotech* 2018, **8**:1–7. https://doi.org/10.1007/s13205-018-1490-x.
in this work it was performed the genome-based analysis of Bacillus velezensis to facilitate our understanding of the mechanism underlying the biodegradation of lignocellulose and the biotechnological application of this novel lignocellulolytic bacteria.

25. Perez CL, Casciatori FP, Thoméo JC: **Strategies for scaling-up packed-bed bioreactors for solid-state fermentation: the case of cellulolytic enzymes production by a thermophilic fungus**. *Chem Eng J* 2019, **361**:1142–1151. https://doi.org/10.1016/j.cej.2018.12.169.

26. Finkler ATJ, Biz A, Pitol LO, Medina BS, Luithardt H, Luz LF de L, Krieger N, Mitchell DA: **Intermittent agitation contributes to uniformity across the bed during pectinase production by Aspergillus Niger grown in solid-state fermentation in a pilot-scale packed-bed bioreactor**. *Biochem Eng J* 2017, **121**:1–12. https://doi.org/10.1016/j.bej.2017.01.011.

27. Mahmoodi M, Najafpour GD, Mohammadi M: **Bioconversion of agroindustrial wastes to pectinases enzyme via solid state fermentation in trays and rotating drum bioreactors**. *Biocatal. Agric. Biotechnol.* 2019, **21**:101280. https://doi.org/10.1016/j.bcab.2019.101280.

28. Poletto P, Polidoro TA, Zeni M, da Silveira MM: **Evaluation of the operating conditions for the solid-state production of pectinases by Aspergillus Niger in a bench-scale, intermittently agitated rotating drum bioreactor**. *LWT - Food Sci Technol* 2017, **79**:92–101. https://doi.org/10.1016/j.lwt.2017.01.018.

29. Rayhane H, Josiane M, Gregoria M, Yiannis K: **From flasks to single used bioreactor : scale-up of solid state fermentation process for metabolites and conidia production by Trichoderma asperellum**. *J Environ Manag* 2020, **252**:109496. https://doi.org/10.1016/j.jenvman.2019.109496.

30. Klein-Marcuschamer D, Oleskowicz-Popiel P, Simmons BA, Blanch HW: **The challenge of enzyme cost in the production of lignocellulosic biofuels**. *Biotechnol Bioeng* 2012, **109**: 1083–1087. https://doi.org/10.1002/bit.24370.

31. Ramesh D, Muniraj IK, Thangavelu K, Karthikeyan S: **Chapter 11 - knowledge update on bioreactor technology for cellulase production**. In *Cellul. To cell. Strateg. To improv. Biofuel prod.*. Edited by Srivastava N, Srivastava M, Mishra PK, Ramteke PW, R.L.B.T.-N., F.D., M.B., Singh B, Eds, Elsevier; 2019:181–193. https://doi.org/10.1016/B978-0-444-64223-3.00011-4.

32. El-Bakry M, Abraham J, Cerda A, Barrena R, Ponsá S, Gea T, Sánchez A, Abraham J, Cerda A, Barrena R, Ponsá S, Gea T: *From wastes to high value added products : novel aspects of SSF in the production of enzymes from wastes to high value added products : novel aspects of SSF in the production*. 2015:3389. https://doi.org/10.1080/10643389.2015.1010423.

33. Arora S, Rani R, Ghosh S: **Bioreactors in solid state fermentation technology: design, applications and engineering aspects**. *J Biotechnol* 2018, **269**:16–34. https://doi.org/10.1016/j.jbiotec.2018.01.010.

34. * * Mitchell DA, Pitol LO, Biz A, Finkler ATJ, de Lima Luz LFJ, Krieger N: **Design and operation of a pilot-scale packed-bed bioreactor for the production of enzymes by Ssolid-state fermentation**. *Adv Biochem Eng Biotechnol* 2019, **169**:27–50. https://doi.org/10.1007/10_2019_90.
In this review, it was described the building of a pilot-scale packed-bed solid-state fermentation bioreactor, with provision for intermittent mixing, and the use of this bioreactor to produce pectinases by filamentous fungi.

35. De Paula RG, Cristina A, Antoniêto C, Maria K, Nogueira V, Fraga L, Ribeiro C, Rocha MC, Almeida F, Silva RN:

Extracellular vesicles carry cellulases in the industrial fungus Trichoderma reesei. *Biotechnol Biofuels* 2019:1–14. https://doi.org/10.1186/s13068-019-1487-7.

36. * Rigoldi F, Donini S, Redaelli A, Parisini E: *Review : engineering of thermostable enzymes for industrial applications*, vol. 11501; 2018:1–17. https://doi.org/10.1063/1.4997367.
reviewed the industrial application of thermostable enzymes.

37. Singhvi MS, Gokhale DV: **Lignocellulosic biomass: hurdles and challenges in its valorization**. *Appl Microbiol Biotechnol* 2019, **103**:9305–9320. https://doi.org/10.1007/s00253-019-10212-7.

38. Mishra V, Jana AK: **Sweet sorghum bagasse pretreatment by Coriolus versicolor in mesh tray bioreactor for selective delignification and improved saccharification**. *Waste and Biomass Valorization* 2019, **10**:2689–2702. https://doi.org/10.1007/s12649-018-0276-z.

39. Perdani MS, Margaretha G, Sahlan M, Hermansyah H: **Solid state fermentation method for production of laccase enzyme with bagasse, cornstalk and rice husk as substrates for adrenaline biosensor**. *Energy Rep* 2020, **6**:336–340. https://doi.org/10.1016/j.egyr.2019.08.065.

40. Catalán E, Sánchez A: **Solid-state fermentation (SSF) versus submerged fermentation (SmF) for the recovery of cellulases from coffee husks: a life cycle assessment (LCA) based comparison**. *Energies* 2020, **13**. https://doi.org/10.3390/en13112685.

41. Saqib AAN, Farooq A, Iqbal M, Hassan JU, Hayat U, Baig S: **A thermostable crude endoglucanase produced by aspergillus fumigatus in a novel solid state fermentation process using isolated free water**. *Enzym Res* 2012, **2012**. https://doi.org/10.1155/2012/196853.

42. Mandal A: *Review on microbial xylanases and their applications*. 2015.

43. Graminha EBN, Gonçalves AZL, Pirota RDPB, Balsalobre MAA, Da Silva R, Gomes E: **Enzyme production by solid-state fermentation: application to animal nutrition**. *Anim Feed Sci Technol* 2008, **144**:1–22. https://doi.org/10.1016/j.anifeedsci.2007.09.029.

44. P. and others Hooge DM, Pierce JL, McBride KW, Rigolin: **Meta-analysis of broiler chicken trials using diets with or without Allzyme® SSF enzyme complex**. *Int J Poultry Sci* 2010, **9**:819–823.

45. Akintunde A, Omole C, Sokunbi O, Lawal T, Alaba O: **Response of growing pigs to diet physical form and Allzyme® SSF supplementation in a palm kernel meal-based diet**. *Anim Prod* 2011.

46. Amin F, Mohsin A, Nawaz H, Bilal M: **Production , thermodynamic characterization , and fruit juice quality improvement characteristics of an Exo-polygalacturonase from Penicillium janczewskii**. *BBA - Proteins Proteomics* 2020, **1868**:140379. https://doi.org/10.1016/j.bbapap.2020.140379.

47. Jayasekara S, Ratnayake R: **Microbial cellulases: an overview and applications**. In *Cellulose*. IntechOpen; 2019. https://doi.org/10.5772/intechopen.84531.

48. da Silva PO, de Alencar Guimarães NC, Serpa JDM, Masui DC, Marchetti CR, Verbisck NV, Zanoelo FF, Ruller R, Giannesi GC: **Application of an endo-xylanase from Aspergillus japonicus in the fruit juice clarification and fruit peel waste hydrolysis**. *Biocatal. Agric. Biotechnol.* 2019, **21**. https://doi.org/10.1016/j.bcab.2019.101312.

49. Karmakar M, Ray RR: **Current trends in research and application of microbial cellulases**. *Res J Microbiol* 2011, **6**:41–53. https://doi.org/10.3923/jm.2011.41.53.

50. Minussi RC, Pastore GM, Durán N: **Potential applications of laccase in the food industry**. *Trends Food Sci Technol* 2002, **13**:205–216. https://doi.org/10.1016/S0924-2244(02)00155-3.

51. Lomascolo A, Stentelaire C, Asther M, Lesage-Meessen L: **Basidiomycetes as new biotechnological tools to generate natural aromatic flavours for the food industry**. *Trends Biotechnol* 1999, **17**:282–289. https://doi.org/10.1016/S0167-7799(99)01313-X.

52. Zhang Y, Yang J, Luo L, Wang E, Wang R, Liu L, Liu J: **Low-cost cellulase-hemicellulase mixture secreted by Trichoderma harzianum EM0925 with complete saccharification efficacy of lignocellulose**. *Int. J. Mol. Sci. Artic.* 2020, **21**:1–18.

53. Csiszár E, Szakács G, Koczka B: **Biopreparation of cotton fabric with enzymes produced by solid-state fermentation**. *Enzym Microb Technol* 2007, **40**:1765–1771. https://doi.org/10.1016/j.enzmictec.2006.12.003.

54. Singh P, Sulaiman O, Hashim R, Peng LC, Singh RP: **Evaluating biopulping as an alternative application on oil palm trunk using the white-rot fungus Trametes versicolor**. *Int Biodeterior Biodegrad* 2013, **82**:96–103. https://doi.org/10.1016/j.ibiod.2012.12.016.

55. Doriya K, Jose N, Gowda M, Kumar DS: *Solid-state ermentation vs submerged fermentation for the production of L-Asparaginase*. 1st ed. Elsevier Inc.; 2016. https://doi.org/10.1016/bs.afnr.2016.05.003.

56. Khanahmadi M, Arezi I, Amiri M, Miranzadeh M: **Bioprocessing of agro-industrial residues for optimization of xylanase production by solid- state fermentation in flask and tray bioreactor**. *Biocatal. Agric. Biotechnol.* 2018, **13**:272–282. https://doi.org/10.1016/j.bcab.2018.01.005.

57. Favaro CP, Baraldi IJ, Casciatori FP: *β -Mannanase Production using coffee industry waste for application in soluble coffee processing*. 2020.

58. Alcântara SR, Honorato da Silva FL: **Optimized polygalacturonase production in reactor tray type, study of enzymatic extraction and extract application**. In *Handb. Food bioeng.*. Edited by Grumezescu AM, A.M.B.T.-S.C., Holban FF, Eds, Academic Press; 2017:233–264. https://doi.org/10.1016/B978-0-12-811412-4.00009-6.