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Advances in biological techniques for sustainable lignocellulosic waste utilization in biogas production

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ARTICLE INFO ABSTRACT

Keywords: Lignocellulosic waste Anaerobic digestion Biogas production Biomethane Biological techniques Improper disposal of lignocellulosic wastes may produce a large quantity of greenhouse gases and pollute the environment. Through anaerobic digestion processes, lignocellulosic wastes can be recycled to produce clean and renewable biogas. However, the lignin in lignocellulose limits its potential as such a biomass resource, and the efficacy of biogas production is not satisfactory although recent research efforts have attempted to address this issue. In this review, the physicochemical characteristics of three lignocellulosic wastes, including municipal solid waste, forestry waste, and crop straw, are summarized. Then, the mechanism and influencing factors of biogas production from these wastes through anaerobic digestion are presented. Biological pretreatment techniques have been confirmed to increase lignocellulose hydrolysis and then enhance biogas production, among them, co-culture systems, metabolic engineering and anaerobic co-digestion are worthy of focus in future research. Furthermore, natural lignocellulose degrading systems, like xylophagous insects and ruminants, also have potential for improving the anaerobic digestion system. This review also considers the future perspective of anaerobic digestion of lignocellulosic wastes, including kinetics and model studies to optimize anaerobic digestion process, and policy to facilitate biogas production from lignocellulosic wastes. This article aims to comprehensively review challenges with anaerobic digestion of lignocellulosic wastes and summarize available pretreatment methods focusing mainly on biological techniques to find efficient and low-cost strategies for improving the anaerobic digestion process and biogas production.

1. Introduction

It is reported that fossil fuels comprise approximately 80% of current global primary energy usage, and fossil fuel based energy systems are primarily responsible for more than two thirds of global greenhouse gas (GHG) emissions [1]. Therefore, developing alternative energies through technological innovation becomes a priority. Anaerobic digestion of biomass into biogas has been given much attention in recent years. Biogas production in 2018 was around 35 million tons of oil

equivalent (Mtoe), only a fraction of the estimated overall potential (730 Mtoe) [2]. It is estimated that the availability of sustainable feedstocks for producing biogas is set to grow by 40% over the period to 2040, which avoids around 1000 million tons of GHG emissions [2].

Lignocellulosic waste materials are available in significant quantities but presently only contribute a limited fraction of biogas output. The most available lignocellulosic waste materials are agricultural byproducts (e.g. crop stalks and straws), wood and branches from forest management and commercial timber production and some fractions of

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Abbreviations: IEA, International Energy Agency; EPA, Environmental Protection Agency; FAOSTAT, Food and Agriculture Organization Corporate Statistical Database; Mtoe, Million tons of oil equivalent; GHG, Global greenhouse gas; WD, Woody debris; MSW, Municipal solid waste; GMO, Genetically modified organism; AD, Anaerobic digestion; CSTR, A continuous flow stirred tank reactor; VFAs, Volatile fatty acids; VS, Volatile solids; PS, Particle size; L/(C + H), Lignin content/ (Cellulose content + Hemicellulose content; I/S, Inoculum to substrate; TMP, Theoretical methane potential; COD, Chemical oxygen demand; BMP, Biochemical methane potential; SW, Softwood; HW, Hardwood; OSB, Oriented strand board; MDF, Medium density fiberboard; AcoD, Anaerobic co-digestion.

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municipal solid waste (e.g. wood, paper and paperboard) [3], which at present are not recovered for biogas generation in significant quantities and could emit GHG if being left to degrade where they are produced or transported to landfill [4,5]. However, the main hurdles in utilizing lignocellulosic waste are presented by the lack of biodegradability of lignin, a limited accessible surface area for enzymatic hydrolysis, and cellulose crystallinity [6-8]. Efficient delignification and improved digestibility of cellulose and hemicellulose in lignocellulosic waste is usually a crucial step of pretreatment. In this respect, biological pretreatment is an attractive pretreatment technology with several significant advantages, including simple operating conditions and equipment, low energy consumption, no or minimum inhibitor formation, and no requirement to remove solvents after pretreatment [9,10]. It has already been widely applied in lab-scale bioreactors or even full-scale biorefinery plants and is gaining in popularity [11,12]. Despite the huge potential, large-scale implementation of biological pretreatment is still constrained by issues such as long pretreatment times, loss of carbohydrates, and low downstream yields [13].

To achieve the technoeconomic feasibility for the large-scale exploitation of biological pretreatment, substantial research efforts remain essential. This review therefore aims to provide an in-depth and critical appraisal of the status of biological pretreatment of lignocellulosic wastes under the following structure: (1) summary of types and content of lignocellulosic waste (Section 2); (2) overview on biogas production from anaerobic digestion of lignocellulosic waste (Section 3), including process mechanisms, major factors affecting biogas production, lignocellulosic waste recalcitrance, and importance of different lignocellulose and fermentation parameters; (3) review of available biotechnology pretreatments for lignocellulosic wastes (Section 4); (4) consideration of economic aspects of biogas production from lignocellulosic waste (Section 5); (5) discussion of challenges, limitations, and perspectives (Section 6).

2. Types of lignocellulosic waste utilized for biogas production

Lignocellulosic biomass comprises dry plant materials and so covers many substances including different grasses, plant stems, trees, and residues from modern sawmills and paper mills. It can be broadly classified into virgin biomass, energy crops and waste biomass. Nearly 200 billion tons of lignocellulosic waste are generated globally every year [14], mostly low value byproduct from various industrial sectors, human activities or the natural environment such as agriculture (e.g. crop straw and stalk), municipal waste (e.g. wood, paper and cardboard) and forestry (e.g. sawmills and paper mills discards, forest management waste). All of these lignocellulosic wastes have been recognized as valuable resources by the U.S. Department of Energy (DOE) [15].

2.1. Municipal solid waste

MSW mainly comprises of commercial wastes, residential wastes and yard wastes generated in municipal areas in either semisolid or solid form excluding agricultural wastes and industrial hazardous wastes but including treated biomedical wastes [16]. The global level of MSW generation is estimated to increase to approximately 2.2 billion tons by 2025 [17]. Low- and middle-income regions produce most MSW, accounting for up to 90.4% of the total [17]. The yearly MSW generation in America and China are highest in the world at 292.36 million tons (2.49 kg per capita per day) and 228.02 million tons (0.45 kg per capita per day), respectively (Fig. 1A) [18,19]. The disposal of MSW depends on national development levels. Landfilling and thermal treatment are valued in high income countries, while composting, and open dumping still account for a large proportion in low- and lower-middle income countries [17]. Fig. 1B shows the data from the Organisation for Economic Co-operation and Development (OECD) [20], U.S. Environmental Protection Agency (EPA) [21] and Eurostat [22], with different countries having very different combinations of waste disposal methods based on their own development and national conditions, however globally sanitary landfilling is currently the dominant MSW disposal method.

In most developing countries, MSW is not segregated at source and is transported into landfill in mixed conditions [23]. An average composition of MSW in different countries is presented in Table 1, showing that there exists a large percentage of lignocellulosic materials and suitable feedstocks for biogas, i.e., paper and paperboard, wood and yard waste. Of these, wood, paper and paperboard wastes are likely to have more recycled value, since they can be reprocessed into particleboard or new cardboard [24]. However, a significant fraction of wood and paper wastes are nonrecyclable with chemical preservatives, binders or metal protectants [25]. The main destination of these lignocellulosic wastes is landfill, Table 2 shows lignocellulosic waste data from 1990 to 2018 in the USA [21]. About 15.6 million tons of wood waste is produced each year, with 71.5% landfilled. An average of 74.2 million tons of paper and cardboard wastes are produced each year, with 36.9% landfilled.

Landfilling, if inappropriately performed or poorly operated, may contaminate the atmosphere with GHG emissions from the slow degradation of lignocellulosic waste. The presence of abundant lignin endows lignocellulosic waste with recalcitrance; it is difficult to break down through microbial action [31]. These poorly degradable fractions are typically associated with a long 'tail' of emissions and gradually accumulate in landfill. Furthermore, these slowly produced gases are insufficient to generate energy and difficult to capture, so the biogas (primarily methane and carbon dioxide) typically escapes into the atmosphere contributing to climate change [32].



Fig. 1. The total generation amount (A) and disposal methods (B) of MSW in different countries [18–22].

Table 1

National average municipal solid waste composition.

Country	Organic (%)	Paper (%)	Plastic (%)	Glass (%)	Metal (%)	Other (%)
Global	46	17	10	5	4	18
Low Income	62	6	9	3	3	17
Lower Middle Income	55	10	13	4	3	15
Upper Middle Income	50	15	12	4	4	15
High Income	28	30	11	7	6	18
China	59	8	10	3	1	19
India	40	10	2	0.2	0	47.8
U·S.	39.9	23.1	12.2	4.2	8.8	11.8
Russia	40	19	14	12	4	11
Brazil	51.4	13.1	13.5	2.4	2.9	16.7
Indonesia	74	10	8	2	2	4
Nigeria	68	10	7	4	3	8
Pakistan	67	5	18	2	0	7
U·K.	46	17	10	7	5	15
Germany	14	34	22	12	5	12
Netherlands	35	26	19	4	4	12
Australia	47	23	4	7	5	13
Mexico	51	15	6	6	3	18
Portugal	34	21	11	7	4	23
Italy	44.5	19.1	8.3	12.3	2	13.8
Spain	44	18	13	9	4	12
Japan	34	34	11.8	4.3	4.7	11.2
Canada	47	15	13	2	3	20

Note: Classification according to Daniel and Perinaz [17]. Organic: food scraps, yard waste, wood, process residues; Paper: paper scraps, cardboard, newspapers, magazines, bags, boxes, wrapping paper, telephone books, shredded paper, paper beverage cups; Plastic: bottles, packaging, containers, bags, lids, cups; Glass: bottles, broken glassware, light bulbs, colored glass; Metal: cans, foil, tins, non-hazardous aerosol cans, appliances (white goods), railings, bicycles; Other: textiles, leather, rubber, multi-laminates, e-waste, appliances, ash, other inert materials. All data are adapted from OECD [20], EPA [21], Statista [26], Ding et al. [27], Khan et al. [28], Millati et al. [29] and Alfaia et al. [30].

Accelerating the degradation of lignin and subsequent methanogenesis in lignocellulosic waste is required to help to confine methane production to a shorter period of higher concentration release, thus allowing more landfill biogas to be collected as energy and preventing low emission of GHG in the long term. This can be addressed with biotechnological methods in two main ways – the application of extracellular enzymes [33–35] or enzyme-producing microorganisms [36–39]. However, these previously mentioned studies have been carried out under laboratory level with highly controlled conditions or standardized materials, scaling-up these technologies to landfill conditions will be highly challenging and is yet to attract significant attention.

2.2. Forestry waste

Forests are the largest terrestrial carbon sink and play a vital role in the global carbon cycle, where plants absorb energy through photosynthesis and store it in wood as carbon [40,41]. The current carbon stock in forests is estimated to be 861 billion tons, with the vast majority in soil (44%) and live biomass (42%) [42]. There are two main types of wood, hardwood and softwood. Hardwoods arise from deciduous trees (e.g. oak, maple, birch) while coniferous trees (e.g. pine, spruce, juniper) produce softwoods. In 2020, global hardwood lumber production reached 2536.7 million m³, mainly in Asia, Africa, the Americas and Europe (Table 3) [43]. Global softwood production was 1375.25 million m³, mostly in Europe and the Americas.

Woody debris (WD), comprising fallen dead trees and the remains of large branches the ground in forests, represents a large carbon pool with carbon stock ranging from 36 to 72 billion tons globally [44]. Unless WD is harvested it will ultimately convert to lignoforms (humus forms formed by the degradation of deadwood) as a part of the soil [45]. In this process of WD being gradually decayed into lignoforms by decomposer communities, most of the carbon is returned to the atmosphere as methane and carbon dioxide [4]. Since methane and carbon dioxide are both greenhouse gases of great concern for climate change [46], this natural process was only recently recognized as an important sources of GHG, with estimates of carbon flux at 8.6 billion tons annually, equivalent to approximately 90% of anthropogenic emissions [47].

Excepting dead wood produced by natural processes, human activities are the main source of WD. The harvesting of approximately 4.3 billion m^3 of wood annually [48] is estimated to generate 232.94 million m^3 of wood waste may be produced in the world every year, mainly in Asia and Europe (Table 3). WD are generated during forestry operations (branches, treetop, leaves, stumps, low grade and decayed wood, slashings, sawdust) and wood processing (bark, sawdust, trimmings, planer shavings, core, screening fines), which also are classed as wood waste. These wood wastes are potential resource for bioenergy

Table 3

Quantity of hardwood and softwood production and residues in 2020.

Types	Production quantity (million m ³)	Waste quantity (million m ³)	Regions
Hardwoods	995.08	102.24	Asia
	760.64	1.56	Africa
	515.78	23.49	Americas
	58.77	0.59	Central
			America
	134.05	5.25	Northern
			America
	317.33	20.05	South America
	231.87	17.57	Europe
	33.34	0.99	Oceania
	2536.7	151.05	World
Softwoods	163.83	16.83	Asia
	30.97	0.06	Africa
	555.14	25.28	Americas
	35.64	0.35	Central
			America
	427.83	16.77	Northern
			America
	91.17	5.76	South America
	571.81	43.33	Europe
	53.5	1.59	Oceania
	1375.25	81.89	World

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1960–2018 Data on MSW lignocellulosic waste in United States (ten thousand tons).

Types Management Pathway 1960 1970 1980 1990 2000 2005 2010 2015 2017 2018 Wood Generated 303 372 701 1221 1357 1479 1571 1630 1820 1800 Recycled - - - 13 137 183 228 266 303 310 Iminantia - - - 13 137 183 228 266 303 310		0		-	-							
Wood Generated 303 372 701 1221 1357 1479 1571 1630 1820 1809 Recycled - - - 13 137 183 228 266 303 310 Incinerate 1 15 208 230 237 231 257 288 284	Types	Management Pathway	1960	1970	1980	1990	2000	2005	2010	2015	2017	2018
Recycled – – – 13 137 183 228 266 303 310	Wood	Generated	303	372	701	1221	1357	1479	1571	1630	1820	1809
Incinenzte 1 15 208 220 227 221 257 288 284		Recycled	-	-	-	13	137	183	228	266	303	310
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		Incinerate	-	1	15	208	229	227	231	257	288	284
Landfill 303 371 686 1000 991 1069 1112 1107 1229 1215		Landfill	303	371	686	1000	991	1069	1112	1107	1229	1215
Paper and paperboard Generated 2999 4431 5516 7273 8774 8484 7131 6805 6701 6739	Paper and paperboard	Generated	2999	4431	5516	7273	8774	8484	7131	6805	6701	6739
Recycled 508 677 1174 2023 3756 4196 4457 4532 4417 4597		Recycled	508	677	1174	2023	3756	4196	4457	4532	4417	4597
Incinerate – 15 86 893 973 780 474 445 449 420		Incinerate	-	15	86	893	973	780	474	445	449	420
Landfill 2491 3739 4256 4357 4045 3508 2200 1828 1835 172:		Landfill	2491	3739	4256	4357	4045	3508	2200	1828	1835	1722

Note: means no data. Data is adapted from US EPA [21].

production that may have a significant impact on the profitability of the entire timber trade value chain, offsetting the negative impacts of forestry operations on ecosystem services and biodiversity. The added value of producing biofuel from these wood waste also comes from reducing fire risk, mitigating forest management costs, and eliminating additional emissions from degradation [49,50].

Direct large-scale combustion of wood waste to generate energy or electricity is no longer considered an efficient and environmentally appropriate option. Thus, attention must be paid to develop alternative options for renewable gaseous biofuel [51]. However, due to the refractory nature of wood waste and immaturity at application level of current anaerobic digestion technology, there are few practical examples of using wood waste fermentation to produce gaseous biofuel. The lignin content in wood is quite high, 25–39% in softwood and 18–25% in hardwood respectively [29], which is not conducive to the degradation process of microorganisms or enzymes. To make fuller use of wood waste to generate more biogas, researchers screen for new high-efficiency lignin-degrading microorganisms [52,53], or use the addition of other nitrogen-rich wastes, such as food waste or animal manure, to create a favorable condition for fermentation [54].

2.3. Crop straw

Agriculture wastes mainly include crop residues and livestock excreta, among which crop straw is a potentially valuable lignocellulosic waste with huge yields. As a by-product of grain production, crop straw is inevitable and its corresponding relationship with grain output is shown in Table 4 [55,56]. Based on the Food and Agriculture Organization Corporate Statistical Database (FAOSTAT) [57], the average annual crop straw production in the world from 2010 to 2022 can be calculated (Table 4). The amount of sugarcane bagasse ranked top in the world at 18575.1 million tons, followed with rice straw, corn straw, wheat straw and barley straw respectively, and the last are cotton and fiber crops. Asia is the region that produces the most food with East Asian countries like China and India major growers of crops [58]. It is estimated that 1000 million tons of crop straw are produced yearly in China [59], while India produces a total of 500 million tons [60].

Crop straw has a low nutritional value and so only a limited amount has been traditionally used as livestock feed with the rest commonly burned in the field or sent to landfills [61]. Open burning of crop straw not only produces particulate matter posing a serial health risk but also is a major cause of environmental pollution, including greenhouse gases and soil fertility destruction [62,63]. Crop straw burning varies by different countries, depending on the type of crop straw and the pattern of its management. Chen et al. claimed that Chinese farmers burned approximately 25% of crop straw [64], while this ratio would rise to 50% in line with FAOSTAT [57]. China, India, United States, Brazil, Russian Federation, Indonesia, Argentina, Nigeria, Ukraine and Thailand are the top 10 countries in terms of quantity of burned crop straw (Table 5). The burning of crop straw leads to inefficient utilization

Table 4

Quantities of crop straw reportedly by region, average 2010-2020 (million tons).

of agricultural waste and an increase in air pollution, which has drawn attention in various parts of the world to develop a proper plan for managing crop straw. Over the past few years, especially since 2015, different international agencies have proposed many avenues to utilize crop straw to minimize crop straw related issues [65].

A core sustainable development goal is the transition to a circular economy, which involves minimizing resource inputs and waste outputs within a closed-loop system pioneering wastes as secondary resources [66,67]. Use of crop straw as material to generate biogas through anaerobic digestion is in line with achieving a circular economy. The biogas production rate of main crop straw residues is shown in Table 6 [55,56]. As a clean renewable energy, biogas can alleviate energy shortages and minimize air pollution risk from the improper management of crop straw. There is little biogas production from agricultural waste currently, although the supply of raw crop straw is plentiful. In India, only 2.07 billion m³ biogas are currently produced per year, though there is the potential for 29–48 billion m³ each year based on straw volume [68]. The biogas industry of China is considered to have great potential, owing to tremendous amount of crop straw. Nevertheless, the ratio of actual biogas production to total biogas potential is only 6.17% [69]. The biogas potential of crop straw is still underexplored due to an imperfect supply chain and viable business models, lack of simple pre-treatment technologies, insufficient short-term returns, and shortage of advanced technology [60]. Many small-scale biogas plants have been operating for decades, although large-scale technically advanced biogas plants are uncommon and a recent development [70]. The priority currently is to improve the biogas potential from crop straw, which could help to eliminate air pollution threats and develop clean energy.

Table 5				
Top 10 countries	of crop straw	burning in	the world	in 2019.

Countries	Biomass burned (million tons)	CH ₄ emission (kilotons)	N ₂ O emission (kilotons)
China	68.2	184.2	4.8
India	48.1	129.9	3.4
USA	39.8	107.3	2.8
Brazil	25.9	69.8	1.8
Russian	13.6	36.8	1.0
Indonesia	11.8	31.9	0.8
Argentina	10.1	27.2	0.7
Nigeria	9.8	26.6	0.7
Ukraine	7.7	20.9	0.5
Thailand	7.5	20.2	0.5

-			•										
Types	Ratio of Straw/Grain	Crop pro	Crop production			Straw production							
		World	Asia	Americas	Europe	Africa	Oceania	World	Asia	Americas	Europe	Africa	Oceania
Rice	1.6	734.8	661.7	36.9	4.2	31.4	0.6	1175.7	1058.7	59.0	6.7	50.2	1.0
Barley	1.0	143.3	21.4	18.7	87.1	6.5	9.5	143.3	21.4	18.7	87.1	6.5	9.5
Corn	0.5	1038.2	325.7	520.0	114.4	77.5	0.6	519.1	162.9	260.0	57.2	38.8	0.3
Wheat	0.7	724.6	321.3	113.4	240.1	25.9	23.9	507.2	224.9	79.4	168.1	18.1	16.7
Sorghum	1.3	60.7	9.0	22.1	1.1	27.0	1.6	78.9	11.7	28.7	1.4	35.1	2.1
Oat	1.3	22.9	1.1	6.2	14.1	0.2	1.3	29.8	1.4	8.1	18.3	0.3	1.7
Beans	0.7	22.0	20.1	0.3	0.9	0.7	0.044	15.4	14.1	0.2	0.6	0.5	0.031
Tubers	2.0	6.8	3.7	0.9	0.1	1.7	0.4	13.6	7.4	1.8	0.1	3.5	0.8
Cotton	0.3	24.9	16.3	5.9	0.3	1.6	0.7	7.5	4.9	1.8	0.1	0.5	0.2
Fiber crops	0.4	0.6	0.4	0.1	0	0.048	0.0042	0.2	0.2	0.1	0	0.019	0.0017
Sugarcane	10.0	1857.5	729.5	1001.8	0.0057	93.2	33.0	18575.1	7295.3	10018.4	0.1	931.9	329.5

Table 6

Dry biomass ratio and biogas production rate of crop straw.

Types of crop straw	Dry matter (%)	Carbohydrates (%)	Biogas yield (m ³ /kg of dry biomass)
Rice straw	88	49.33	0.43
Barley straw	81	70.00	0.48
Corn straw	78.5	58.29	0.46
Wheat straw	90.1	54.00	0.45
Sorghum straw	88	61.00	0.41
Oat straw	89.1	59.10	0.40
Beans straw	80	54.48	0.40
Sugarcane bagasse	71	67.15	0.43

3. Biogas production from anaerobic digestion of lignocellulosic waste

3.1. Process mechanisms

Anaerobic digestion (AD) decomposes lignocellulosic feedstocks into biogas in four stages: hydrolysis, acidogenesis, acetogenesis and methanogenesis [71] (Fig. 2). These steps are a synergistic process of diverse microbial groups, and bacterial metabolic activities at different stages mutually affect each other, in close dependence on each other.

The AD process starts with hydrolysis, at this stage hydrolytic anaerobic and facultative bacteria produce extracellular hydrolases that destroy the cellulose-hemicellulose-lignin structure and then convert complex polymeric organics to soluble monomers [71,73]. In acido-genesis, the reduced monomers (amino acids, peptides, long-chain fatty acids, glycerides, and sugars) are further degraded by facultative aerobes to volatile fatty acids (VFAs) (53–58% acetic acid, 6–13% propionic acid and 30–35% butyric acid) and other minor products (alcohols, al-dehydes, hydrogen, and carbon dioxide) [74,75]. During acetogenesis, syntrophic bacteria transform previous VFAs and alcohols into acetate, carbon dioxide, and hydrogen which are substrates for the production of methane [72,74]. The final step is methanogenesis, where methanogene methane, mainly consisting of acetoclastic methanogenesis (60–70%) and hydrogenotrophic methanogenesis (about 30%) [72,76].

3.2. Major factors affecting biogas production

Since all four stages take place in one bioreactor, AD is a fragile biological process that can easily be disrupted resulting in activity



Fig. 2. Degradation pathways during anaerobic digestion of lignocellulosic waste, modified from Ref. [72].

inefficiency or even complete failure. The equilibria of AD depend on feedstock characteristics [77,78], temperature [79,80], pH [81], microbial community [82], solid-liquid ratio [83], inhibitory compounds [84], etc. In general, temperatures of 10-65 °C [85], pH of 5.0-8.5 (5.5-7.0 for hydrolysis and acidogenesis, 6.8-8.5 for methanogenesis) [85,86], C/N ratios of 20-35 [87,88] and solids loadings of 20-40% [89] are the optimal ranges for methane yield. Temperature range can vary widely during AD, and it is divided into three categories according to the microbial activity, psychrophilic: 10-20 °C; mesophilic: 20-45 °C (usually 37 °C); and thermophilic: 50-65 °C (usually 55 °C) [85,90]. Compared to the effect of temperature, pH plays a more important role in AD. Anaerobic fermentation bacteria, especially methanogens, are sensitive to the acid concentration in the system. The growth of methanogens could be inhibited at lower pH conditions, and the optimal pH for methanogenesis has been found to be around 7.2 [91]. Improper C/N ratios will result in the release of a large amount of ammonia nitrogen or the excessive accumulation of volatile fatty acids, which are inhibitors in anaerobic digestion process [92]. Therefore, an appropriate temperature, pH and C/N ratio are needed for maintaining a stable environment in a long-term operation.

While temperature, pH, and C/N ratio can be adjusted by controlling the operating conditions, reactor configuration, and the concentrations of N-containing additives [93-95], feedstock characteristics have specific impacts on methane production. Feedstock characteristics include chemical composition [96], volatile solids (VS) content [97], chemical oxygen demand (COD) [98], morphology (particle size and porosity) [80], and nutrient content [54]. These characteristics relate to initiation rate, biodegradability of components, VS conversion rate, hydraulic retention time, and ultimately impact biochemical methane potential (BMP) [72]. In lignocellulosic waste, cellulose and hemicellulose are the major contributors to methane formation. They are easily degraded because of their less complicated molecular structure [99]. However, the presence of lignin limits methane production by reducing the surface area that bacteria can access through а rigid lignin-cellulose-hemicellulose matrix or high cellulose crystallinity, thereby suppressing biodegradability of other components [3,100]. In addition, the decomposition of lignin produces inhibitors, such as phenolic aldehydes and acids, which may also inhibit the methanogenesis process [101].

3.3. Lignocellulosic waste recalcitrance

An extensive range of protein-rich or fat-rich wastes are the usual target for anaerobic digestion, however, less digestible lignocellulosic components are rarely exploited due to low energy extraction efficiency. Lignocellulosic biomass, formed from lignin, cellulose, and hemicellulose, presents barriers to degradation through the structure of individual components and also their combined form. Barriers arise from the interconnection between cellulose, hemicellulose, and lignin, forming a complex and undegradable lignocellulosic matrix [102].

Cellulose is an unbranched biopolymer of β -1,4 glucan, whereas hemicellulose is a heterogeneous polymer of various sugars. The glucose chains in cellulose do not exist independently and tend to produce three-dimensional microfibrils with a high degree of polymerization through van der Waals interactions and hydrogen bonds [103]. Each glucose unit is hydrogen-bonded with two intra-chains and two or three inter-chains. These hydrogen bonds give cellulose its crystallinity, which makes it structurally stable and tightly packed.

The recalcitrance of lignin has been a major obstruction for the utilization of lignocellulosic wastes. Lignin requires high temperatures and high acidity to be dissolved and considered as the most stubborn component in lignocellulose [104]. It has been widely believed that the higher the lignin content, the more recalcitrant the biomass is. Lignin is structurally composed of three hydroxycinnamyl alcohol monomers, including coniferyl, *p*-coumaryl and sinapyl alcohol, with a variety of ethers and C–C bonds [105]. Once incorporated into the lignin polymer,

these substituents are distinguished by aromatic ring structures and called guaiacyl, p-hydroxyphenyl and syringyl substituents. Besides the content, variation in the quantity of these components has a significant impact on delignification chemistry and therefore on biomass decomposition. Guaiac lignin is reported to be more likely to C-C cross-link at C-5 position, which cannot be hydrolyzed by acids or bases, leading to their ability to prevent fiber swelling and enzyme accessibility [106]. The lignin crust has been identified as a challenge in the hydrolysis of lignocellulose because it limits the accessible surface area of polysaccharide hydrolases to substrates. Lignin crosslinks with cellulose and hemicellulose to forms a 'glue-like' structure (Fig. 3A), which effectively prevents microorganisms and enzymes from attacking easily degradable parts, thereby further limiting the biogas potential of lignocellulosic waste [107]. Lignin also is a source of compounds, vanillic acid and syringyl aldehyde, which could inhibit hydrolases and fermentation organisms [108]. In summary, the recalcitrance of lignocellulosic biomass is influenced by several factors, i.e., lignin barrier, cellulose crystallinity, and accessible surface area.

3.3.1. Chemical composition

Lignocellulosic waste is composed primarily of lignin, cellulose, hemicellulose (together accounting for 90% weight by dry mass), along with a small quantity of proteins and minerals [3]. Table A1 and Fig. 4 show the content of major components in different lignocellulosic wastes. The lignocellulose composition of wood or wood products, like oriented strand board, particleboard, plywood and medium density fiberboard, are similar, with a lignin content between 25% and 40% (average of about 28.8%). In contrast, the cellulose content in paper and paperboard is up to 68.6%, and crop straw is high in hemicellulose with an average value of 27.6% (Fig. 4). Both paper, paperboard and crop straw have relatively low levels of lignin (approximately 10%), and the lignin content varies widely among the different types of crop straw, ranging from a minimum content of 5.2% in maize straw to a maximum content of 26.7% of wheat straw (Table A1).

3.3.2. Linkages of different components

Cellulose is a homogeneous long-chain polymer composed of repeating D-glucose units linked by β -1,4 glycosidic bonds. These glucose monomers are present in the pyranose of a cellulose chain with six-carbon rings, and two pyranoses being connected to each other by acetal linkages [111]. Hemicellulose is a heterogeneous polysaccharide composed of arabinose, xylose, glucose, galactose, mannose and sugar acids. These monomers are bonded to each other through glycosidic and fructose ether linkages, forming a branched polymer structure [3,112]. In lignocellulose, lignin occupies the free space between cellulose and hemicellulose and crosslinks with cellulose and hemicellulose to form a

rigid structure (Fig. 3A). Lignin has a helical structure formed by the polymerization of three phenylpropane monomer units, which are connected by ether and carbon-carbon linkages [113,114]. In addition, cellulose, hemicellulose, and lignin are interconnected to form numerous intrapolymer and interpolymer cross-linkages, mainly including hydrogen, ether, and ester linkages. Table 7 lists the different intrapolymer and interpolymer linkages [115], Fig. 3B shows the linkages within lignin molecule and between lignin and other components.

3.4. Performance of different lignocellulose and fermentation parameters

The chemical composition of the feedstock and fermentation parameters have a large impact on methane production, Table B1 summarizes many typical cases of biomethane production from anaerobic digestion of different lignocellulosic wastes. To explore the connection in detail, a mesophilic fermentation (about 37 °C) with the following parameters fixed, initial pH of AD (about 7), AD time (30-50 d), inoculum (sludge) was selected, which were the commonly used conditions in anaerobic digestion of lignocellulosic waste. There is a highly positive correlation between methane and biogas yield (Fig. 5A and B). Additionally, lignin content and L/(C + H) show a moderate negative correlation with methane yield, revealing that the presence of lignin could limit anaerobic digestion of lignocellulosic wastes (Fig. 5A). Wastes with single components, such as crop straws and plant residue like peel and reed, have the highest methane yield of lignocellulosic wastes at 161.2 and 191.8 mL/g VS. The methane yield of mixed woody wastes, yard wastes and leaves are 121.8 and 65.9 mL/g VS, respectively. However, co-digestion could optimize the chemical composition of feedstock and C/N ratio, finally improve methane yield (236.7 mL/g VS) (Fig. 5C).

At different C/N and I/S ratios, the fitting curves of feedstock lignocellulose composition and methane production show that cellulose and hemicellulose are positively correlated with methane production overall (Fig. 6). It is worth noting that at the recommended C/N ratio (25-30), the content of lignin is also positively correlated with methane production (Fig. 6C). Biogas yield is generally determined by lignin content and C/N ratio. Under standard temperature and pressure conditions, the methanogenesis potential of lignin (727 mL/g VS) is much higher than that of cellulose (415 mL/g VS) and hemicellulose (424 mL/ g VS) [117]. In general, lignin limits methane production, but pretreatment can increase the utilization of lignin in lignocellulosic waste, for example, through the co-digestion with other nitrogen-rich wastes to achieve the best fermentation C/N ratio of materials. At the recommended C/N ratio (25-30), some studies used NaOH solution for pretreatment (Table B1). Alkali pretreatment is considered as an effective method for maximizing degradation of complex materials, in breaking ester bonds between lignin and other compounds along with preventing



Fig. 3. (A) Spatial arrangement of lignin, cellulose, and hemicellulose in lignocellulosic biomass, modified from Ref. [7]. (B) Different types of linkages within lignin molecule and between lignin and other components, modified from Refs. [109,110].



Fig. 4. The chemical composition of different lignocellulosic wastes plotted from the data in Table A1. A: Cellulose content (%); B: Hemicellulose content (%); C: Lignin content (%). Lignocellulosic waste types are distinguished by color. Black dashed lines represent the average value for each waste type. Softwood (SW); hardwood (HW); oriented strand board (OSB); medium density fiberboard (MDF).

Table 7				
The cross-linkages	among cellulose,	hemicellulose	and	lignin

Cross-linkages	Types of bonds	Components
Intrapolymer	Ether Ester Hydrogen Carbon to carbon	Lignin, hemicellulose, cellulose Hemicellulose Cellulose Lignin
Interpolymer	Hydrogen Ether Ester	Cellulose-hemicellulose Lignin-cellulose Lignin-hemicellulose

hemicellulose fragmentation [118]. The availability of lignin components was improved by alkali pretreatment, and thus the methane yield tended to increase with lignin content (Fig. 6C), which is consistent with the results of previous research [119]. Methane yield showed a negative correlation with lignin content, whatever the variation of I/S ratio (Fig. 6F). Yin et al. reported lignin inhibits the utilization of substrate (acetate) by bacteria in anaerobic digestion sludge, leading to lower methane production, and this inhibition effect enhanced with the increase of lignin content. Moreover, this inhibition could not be compensated by adding more acetate in the early stage [120]. In combination with microbiome studies in sludge, this situation may be due to the fact that the main microbial components in sludge do not have the ability to biodegrade lignin [121,122], therefore the availability of substrate decreases as lignin content increases.

4. Available biotechnology pretreatments for lignocellulosic wastes

The process of recovering energy from lignocellulosic waste generally involves pretreatment. There are many pretreatment technologies for lignocellulosic waste, which can be divided into physical pretreatment, chemical pretreatment, and biological pretreatment [123]. The purpose of all pretreatment technologies is to disintegrate lignin, cellulose, and hemicellulose as completely as possible, producing smaller fragments that are easily accessible to enzymatic hydrolysis or other biorefining processes for higher yields of added-value products (Fig. 7). In AD plants that consume lignocellulosic materials, the cost of the pretreatment process typically exceeds 40% of budget [9]. Although pretreatment technologies have been studied for many years and continuously improved, each method still suffers from obvious pitfalls in practice. For example, physical pretreatments such as grinding, steam



Fig. 5. (A) The correlation between parameters and product yield. (B) Curve fitting between methane and biogas yield. (C) Methane yield of different lignocellulose types (delete data containing pretreatment process). All figures are plotted from the data in Table B1. Lignocellulosic waste types are distinguished by color. Black dashed lines represent the average value for each waste type. L/(C + H): Lignin content/(Cellulose content + Hemicellulose content); LCH: Lignocellulose content (%) = Lignin content + Cellulose content + Hemicellulose content; VS: Volatile solids; PS: Particle size; I/S: inoculum (sludge) to substrate; TMP: theoretical methane potential (mL/g VS) were calculated according to the lignocellulose content [116].

explosion, ultrasound, microwave or thermal are energy-intensive and not cost efficient. Similarly, the application of chemicals like alkalis, acids or ionic liquids in pretreatment is faster but will generate wastewaters and toxic substances that require extra financial expenses for chemicals recycling. In contrast, the biological pretreatment, despite being a comparatively slower process, is a cost-effective technique that requires low energy input and is relatively free of hazardous chemicals [124,125]. However, the effect of biological pretreatment methods is currently not ideal due to limited technology. For example, the rapid and profitable production of cellulase has not yet been achieved. Nonetheless, scholars are increasingly interested in applying microorganisms or enzymes for pretreatment, with continuous attempts to screen suitable microbial communities with diverse enzymatic components and efficient hydrolysis activities.

In contrast to other techniques, biological pretreatments including enzymatic, fungal, and bacterial pretreatment, could be alternative options with low energy input and lower waste production. A broad range of microorganisms and their hydrolases found naturally can be used for biological pretreatment. In addition, there are many kinds of microorganisms that can degrade lignocellulose in the gut of xylophagous or saprophagous insects, so these insects offer a potential alternative for pretreatment. All in all, lignocellulose is difficult to be utilized as a lownutrient resource, but many organisms have evolved systems in response to the fierce competition for food in nature that are capable of extracting value and energy. This section focuses on the status and development of biological pretreatment technologies for lignocellulosic waste recovery in recent years, especially those with potential applications. Examples of these pretreatments are described in Table 8, and the characteristics of these biotechnologies are shown in Fig. 7.

4.1. Lignocellulose degrading enzymes

To fully decompose lignocellulosic materials in pretreatment, the most direct and effective method is the application of enzymes because they can be selected specifically for the waste components, and the functions of different enzymes are affected by environmental conditions rather than affecting each other. There are three main types of enzymes, ligninolytic enzymes, cellulolytic enzymes and hemicellulolytic enzymes, that can be used depending on the composition of lignocellulosic waste [125]. Lignin is a complex and stubborn substance, and its degradation usually begins with an oxidation process, so ligninolytic enzymes include several oxidases including laccases, lignin peroxidase, manganese peroxidase and versatile peroxidase [150]. Fungi such as white rot fungi, brown rot and soft rot fungi are well-known producers of ligninolytic enzymes [151], while bacteria are considered to have low potential for lignin degradation. However, Bugg et al. believed bacteria



Fig. 6. Curve fitting between methane yield and feedstock lignocellulose composition under different C/N and I/S. A and D: Cellulose content (%); B and E: Hemicellulose content (%); C and F: Lignin content (%). All figures are plotted from the data in Table B1.

also play a role in producing ligninolytic enzymes and reviewed that actinomycetes, α -proteobacteria, and γ -proteobacteria are able to break down lignin [152]. Cellulolytic enzymes consist of endocellulases, exocellulases and cellobiases (β -glucosidases); these hydrolases can catalyze cellulose into monomeric sugar units through synergistic action. Endoand exo-cellulases hydrolyze internal bonds in cellulose chains to release cellobiose, and β -glucosidases further cleaves cellobiose to glucose [153, 154]. Hemicellulolytic enzymes include glycoside hydrolases and carbohydrate esterases, where glycoside hydrolases hydrolyze glycosidic bonds and carbohydrate esterases hydrolyze ester linkages of ferulic acid or acetate groups [125]. These hemicellulolytic enzymes act synergistically in the hydrolysis of hemicellulose into several monomeric sugars [155]. Besides, polysaccharide monooxygenases discovered in recent years can assist cellulolytic and hemicellulolytic enzymes by oxidative disintegration of recalcitrant polysaccharide chains [156].

A number of studies focus on the application of enzymes for pretreatment. Kim et al. reported a technology for the pretreatment of livestock manure using pancreatin, secreting from the pancreas and containing a variety of digestive enzymes, and the results showed that hydrolysis efficiency and biogas yield were significantly improved [116]. Researchers invented two-stage combination strategies that combines enzymes with other techniques to improve the pretreatment process. Singh demonstrated a pretreatment technique combining chemical, physical or thermal approaches with enzymes widely used in lignocellulosic materials [157]. In another study, Wieczorek et al. found that enzymes (Onozuka R-10 and Macerozyme R-10) can facilitate the fermentation process of microalgal biomass resulting in an approximately 2-fold and 7-fold increase in methane and hydrogen yield, respectively [133]. Overall, other pretreatment techniques are required for lignocellulosic waste prior to enzymatic processing to increase hydrolysis rates and sugar yields. A successful high sugar yield enzymatic process requires a sterilization step to eliminate the consumption of released sugars by endogenous microorganisms prior to AD [158]. These additional steps could limit the industrial application of enzymatic pretreatment by imposing costs. Furthermore, the profitability of enzymatic pretreatment technologies essentially rely on the supply of low-cost enzyme sources. Although a variety of fungi (white rot fungi and brown rot fungi) have been investigated as an economical source of enzymes, the costs of commercial enzyme preparations are still high [159,160].

4.2. Microbial community construction

4.2.1. Fungal communities

Fungi are well known for their enzymatic degradation of lignocellulosic biomass, these fungi can produce various ligninolytic [161,162], cellulolytic [163], and hemicellulolytic enzymes [163]. Lignocellulolytic fungi include ascomycetes (*Aspergillus* sp., *Trichoderma reesei*), basidiomycetes (*Schizophyllum* sp., *Phanerochaete chrysosporium* and *Fomitopsis palustris*) and a few anaerobic species (*Orpinomyces* sp.) [125], of which studies have primarily focused on white-rot and brown-rot fungi [12]. White-rot fungi have been found to be the most effective in disintegration of lignin, because of various ligninolytic extracellular oxidases such as laccases, lignin peroxidases, versatile peroxidases, copper-dependent laccases and manganese peroxidases [164]. Some white-rot fungi, like *Ceriporiopsis subvermispora*, *Phellinus pini*, *Phlebia* sp. and *Pleurotus* sp., preferentially attack lignin rather than holocellulose



Fig. 7. The goals of pretreatment to overcome lignocellulose recalcitrant and characteristics of different biotechnologies.

(cellulose and hemicellulose) to delignify wood, leaving cellulose-rich materials. After delignification by white rot fungi, the decayed wood is whitish in color and fibrous in texture [165]. Unlike white-rot fungi, brown-rot fungi mainly utilize polysaccharides in lignocellulose while partially delignifying, resulting in shrinkage of the wood and a brown discoloration of oxidized lignin [166]. Other fungi degrade cell walls mainly through holocellulose, it is reported that *Trichoderma reesei* secretes xylanases and β -glucosidase which have high cellulase activities [125].

In a study of 30 bacterial and 18 fungal lignocellulolytic enzymes comparing their saccharification activities for lignocellulosic wastes [136], the overall activities of fungal hydrolases were more than twice that of bacteria. Fungal pretreatments are performed in an aerobic solid state fermentation system, requiring low bioreactor volume and less water. Results from several lab-scale studies investigating the effect of fungal pretreatment on BMP of various lignocellulosic wastes generally showed significant increases in methane yield, reaching 50% or higher, even in feedstocks with very low biodegradability [12]. Sindhu et al. found that fungal pretreatment could boost hydrolysis efficiency by 7–20 times, achieve 44–50% lignin removal, and completely eliminate any requirement for hazardous chemicals [9]. Although the lignin degradation pathway in fungi has been extensively studied since the late 1980s, there is as yet no breakthrough in its commercial application.

mainly due to the practical challenges of bioengineering operability in complex fungal genomes.

4.2.2. Bacterial communities

Many bacteria secrete degrading enzymes that can decompose lignin, the selection of most efficient strains for pretreatment of lignocellulosic waste is the crucial step during biogas production. It is reported that DypB from Rhodococcus jostii RHA1 is a lignin peroxidase that is able to oxidize both polymeric lignin and a lignin model compound [132]. With advances in biotechnology, more and more bacteria have been identifying with the ability to degrade lignin through assays involving ¹⁴C-labelled lignin, fluorescently labelled lignin or chemically nitrated lignin [167,168], and exist in three classes: actinomycetes, α -proteobacteria, and γ -proteobacteria [169]. Bugg et al. reviewed all four kinds of bacterial enzymes for lignin depolymerization, including Dyp-type peroxidase enzymes, multi-copper oxidase enzymes (laccases), manganese superoxide dismutase enzyme, and glutathione-dependent β -etherase enzymes [170]. By analyzing the genome sequences of 13 lignin-oxidizing bacteria, Granja-Travez et al. found that Dyp-type peroxidase enzymes and multi-copper oxidase enzymes are ubiquitous in the genomes of lignin-degrading bacteria, and the β-ketoadipate pathway appears to be the most common route for aromatic metabolism [171]. Unlike lignin, cellulose and hemicellulose are relatively easier to

Table 8

The biological pretreatments for valorization of lignocellulosic biomass.

Categories	Feedstocks	Biological technologies	Major benefits	Ref.
Fungi	Bamboo culms	Punctularia sp. TUFC20056	>50% lignin degradation	[126]
	Sawdust	Pleurotus ostreatus; Pleurotus pulmonarius	20 folds enhanced hydrolysis	[9]
	Wheat straw	Ceriporiopsis subvermispora	Enhanced hydrolysis	[127]
	Hardwood and straws	Ceriporiopsis subvermispora	Enhanced delignification	[128]
	Sugarcane bagasse	Aspergillus niger	High endoxylanase activity	[129]
Bacteria	Wood	Petronet alfa and Petronet omega	205% enhanced hydrolysis and 88.9% enhanced	[130]
			biomethane production	
	Pine	Agrobacterium sp.	Enhanced delignification and 10 folds enhanced	[131]
			biomethane production	
	Kraft lignin	Rhodococcus jostii RHA1	Enhanced delignification	[132]
Enzyme	Newspaper	Lignin peroxidase	Enhanced breakdown of lignocellulose and 41%	[98]
			enhanced biomethane production	
	Livestock manure	Pancreas	Enhanced hydrolysis and biogas production	[116]
	Microalgae	Onozuka R-10; Macerozyme R-10	Enhanced hydrolysis efficiency	[133]
Co-culture	Sugarcane bagasse	Clostridium thermocellum +	Enhanced hydrolysis efficiency	[134]
		Thermoanaerobacterium aotearoense		
	Corn stover	Bacillus amyloliquefaciens + Trichoderma asperellum	Enhanced hydrolysis efficiency	[135]
	Pine	Bacterial consortium	5-10 folds enhanced biogas production	[131]
	Sawdust	Microbial consortium	56.7% of lignin removal and 72.6% enhanced	[52]
			biomethane production	
	Crop straws	Co-culturing of bacteria and fungus	3–6.6 folds enhanced hydrolysis	[136]
Metabolic engineering	Corn stover	Overexpression of Trvib-1 in Trichoderma reesei Rut-C30	Enhanced sugar release	[137]
	N/a	stk-12 deletion in Neurospora crassa	Enhanced cellulase production	[138]
	N/a	Xylose-isomerase pathway expression of	Enhanced xylose utilization	[139]
		Saccharomyces cerevisiae	•	
	Corn stover	Vel1 overexpression of Trichoderma asperellum	Enhanced hydrolysis efficiency	[135]
Anaerobic co-digestion	Corn Stover	AcoD of swine manure	Enhanced biomethane yield	[140]
(AcoD)	Lignocellulosic biomass	AcoD of poultry feces	Enhanced biogas yield	[141]
	Lignocellulosic wastes	AcoD of food waste	Reduced hydraulic retention time and enhanced	[142]
	0		biomethane vield	
	Straws	AcoD of bagasse	Enhanced biogas yield	[143]
	Grass	AcoD of forbs	Enhanced biomethane yield	[144]
	Agricultural wastes	AcoD of slaughter residues	Enhanced biomethane vield	[145]
	Different lignocellulosic	AcoD of residual sludge	Enhanced biomethane yield	[146]
	wastes	0	•	
	Oat straw	AcoD of Tannery Wastes	60% enhanced biogas yield	[147]
Natural lignocellulose	Corn silage and cattail	rumen fungus	Enhanced ch4 production	[148]
degrading systems	Straws	Rumen bacteria	Enhanced hydrolysis and biogas yield	[37]
	Straws	Rumen	1.2–1.4 folds enhanced biogas production	[149]
	Paper, yard and wood	termite hindgut microorganism	49% enhanced biomethane production	[36]

degrade. For example, *Clostridium* and *Bacteroides* are capable of cellulose degradation [11], whilst *Thermomonospora fusca*, *Cellulomonas fimi* [125], various gram-positive strains (*Firmicutes*) and gram-negative strains (*Pseudomonas*, *Rahnella* and *Buttiauxella*) have been found to produce cellulases and show activity in degrading cellulosic materials [172].

Although bacterial lignin-degrading enzymes are less studied and characterized compared to fungi, with the maturity of omics technologies it is becoming clear that bacteria have a variety of degrading enzymes with potential in the pretreatment of lignocellulosic waste. Rashid et al. screened out a facultative anaerobic bacterium, Agrobacterium sp., from landfill soil with strong lignin degradation ability [131], then Muaaz-us-Salam et al. applied it in lignocellulosic waste pretreatment resulting in a 2-fold increase in biogas yield [98]. Bacteria are the main contributors to methane production during the anaerobic fermentation process, so the simplest strategy of biological pretreatment is to add bacteria for enhanced hydrolysis prior to anaerobic fermentation. Mirmohamadsadeghi et al. reported the impact of various pretreatments on anaerobic microbial diversity which can markedly affected biogas yield [82]. After applying different microbial inocula the microbial community in the fermentation process under the same conditions will remain different [173]. Microbial consortium TC-5, which included Ruminiclostridium (63%), Thermoanaerobacterium (23%), and Caproiciproducens (12%) and showed a variety of lignocellulolytic enzyme activity, was able to increase methane production by 22-36% during anaerobic digestion of untreated wheat straw [174].

4.2.3. Microbial co-culture systems

Due to the diverse composition of feedstocks, a complex enzymatic system is required for hydrolysis of lignocellulosic materials and methanogenesis fermentation processes. A single strain of any bacterium or fungus cannot simultaneously produce all required enzymes to achieve the desired effect, and microbial co-culture systems was thus proposed [175]. Although it is challenging for microorganisms with different degradation targets to survive and perform their functions together under the same culture medium, several co-culture systems have been found. A co-culture system is an ideal approach for one-step fermentation from lignocellulosic waste and offers several important advantages in constructing efficient bioproduction processes. Compared to microbial monoculture, co-culture systems can reduce the metabolic burden of each constituent strain and help to improve overall performance [176]. They also provide diversified cellular environments, which is conducive to the expression of hydrolases synthesized by different pathways and reduces the interference between different working modules [177,178]. There are three general co-culture systems in pretreatment process: bacterial co-culture, fungal co-culture, and bacterial and fungal co-culture [125].

In an example of bacterial co-culture systems, common cellulolytic bacteria are *Clostridium cellulovorans*, *Clostridium cellulolyticum*, and *Clostridium thermocellum*, that secrete various cellulases enzymes working together in cellulose hydrolysis [11]. Kato et al. also observed higher cellulose degradation in a mixed culture of *Clostridium straminisolvens* and three other aerobic non-cellulolytic bacteria [179]. Chandra et al.

found that Paenibacillus sp., Aneurinibacillus aneurinilyticus, and Bacillus sp. degraded kraft lignin by 37%, 33% and 30% respectively, while the mixed culture of these three bacteria reduced colour by 69%, lignin by 40% and total substrate by 50% under the same conditions [180]. Moreover, researchers experimented with mixed cultures of rumen bacteria, looking for possible combinations of high enzymatic activity to improve the degradation of lignocellulosic waste [181,182]. Culture of two or more species of fungi in pretreatment of lignocellulosic waste has been practiced for decades, with fungal co-cultures resulting in better enzymatic composition. There is considerable evidence for improved cellulolytic activity in fungal co-cultures. The mixed culture of Trichoderma reesei and Aspergillus phoenicis showed high levels of total cellulase and β -glucosidase production at 27 °C and pH of 5.5 [183]. Taha et al. compared the cellulase and xylanase activities of 30 isolated bacterial and 18 fungal strains by feeding four different straw substrates, then selected four fungal and five bacterial isolates based on their high enzymatic activities to construct dual and triple microbial panels. The results showed that fungal co-culture or bacterial co-culture increased hydrolysis efficiency by 2.8-6.6 times [136]. Furthermore, Chi et al. found high lignin degradation in the co-culture of Ceriporiopsis subvermispora and Pleurotus ostreatus [184]. Due to contrasting culture conditions (aerobic for fungi, anaerobic for lignin-degrading bacteria), few studies have focused on bacterial and fungal co-culture. In this co-culture pretreatment, fungi reduce the recalcitrance of lignin and hydrolyze holocellulose into soluble sugars, which are further converted by bacteria into valuable products.

However, finding suitable microbial co-culture systems is a long and arduous task because they have different genetic material, population size and ecological niches. Microorganisms performing different functions living in the same system may compete with each other for resources and fail to maximize their metabolic functions. At the same time, microbial communities living in natural habitats have extremely intricate food web networks, and it is difficult for most microorganisms to be cultivated artificially, which also reduces the available sources of microorganisms. Fortunately, the genetic makeup of bacteria enables them to rapidly adapt to new environments or to improve adaptive traits within their existing ecological niches [185]. Through domestication in highly competitive and hostile environments, combined with 16S rRNA gene sequencing, a co-culture system for efficient lignocellulose pretreatment can be obtained. Ali et al. isolated a novel microbial consortium using sterilized wood as a sole energy source, and biological pretreatment showed effective biodegradation in cellulose, hemicellulose, and lignin (37.5%, 39.6%, and 56.7%, respectively). Pretreatment increased biogas production by 72.6% after 28 days of anaerobic fermentation [52].

Overall, microbial co-culture systems for pretreatment have the potential to be combined with anaerobic digestion. However, detailed biochemical characterization of the various co-culture microorganisms involved in the conversion of lignocellulose to biogas is required to construct compatible and efficient systems for both pretreatment and anaerobic digestion processes.

4.2.4. Metabolically engineered microorganisms

In general, microbial species used for pretreatment have been improved through random mutagenesis and screening processes, but these processes are largely slow, unpredictable and limited by microbial intrinsic phenotype. Therefore, metabolic engineering for purposeful enhancement of microbes attracts considerable attention [186]. To boost biogas production, a comprehensive understanding of the metabolic pathways of the microbial communities is the primary prerequisite. High throughput metagenomic sequencing is used to identify the genetic components of various microorganisms from different environments that contribute significantly to biofuel production, and bioinformatics tools and gene editing techniques enable targeted microbial improvements to boost biogas production [187,188].

Metabolic engineering can provide microorganisms with higher

productivity and product diversity. Overexpression of *Trvib-1* in *Trichoderma reesei* increased its cellulase production by 200%, while a 40% increase in corn stover hydrolysis was observed [137]. Karuppiah et al. reported that by overexpressing *Vel1* in *Trichoderma asperellum* and co-culturing it with *Bacillus amyloliquefaciens*, higher enzymatic activity and 90% hydrolysis efficiency were achieved [135]. Moreover, the process of biofuels recovery from certain lignocellulosic waste can be simplified through metabolic engineering. Rollin et al. combined more than 10 purified enzymes into artificial enzymatic pathways, achieving high yields from glucose and xylose to hydrogen [189]. Furthermore, metabolic engineering allows microorganisms to utilize cheap feed-stocks, reducing the cost of fuel production. *Saccharomyces cerevisiae* cannot grow on xylose and thus cannot efficiently utilize lignocellulosic waste [190], thus many studies have improved the xylose utilization rate of *Saccharomyces cerevisiae* through metabolic engineering [190].

In addition to enhancing the hydrolysis ability of the microorganism itself through genetic modification, it is also an effective approach to introduce the genes encoding lignocellulose hydrolase into non-hydrolyzed microorganisms of high growth yield [187]. Sedlak et al. introduced three xylose metabolizing genes (xylose reductase, xylitol dehydrogenase and xylulokinase) into *Saccharomyces* yeast through metabolic engineering to enable glucose and xylose co-fermentation [191]. Divia et al. used recombinant DNA technology to develop anaerobic bacteria with enhanced hydrolysis properties that could reduce hydraulic retention time and increase biogas yield [192].

Although metabolic engineering can certainly enhance beneficial characteristics such as hydrolysis performance of microorganisms to increase methane production, industrial-scale applications of genetically modified strains may be limited by the regulations of genetically modified organisms (GMO) [193]. In view of this, isolation of naturally hydrolyzing microorganisms and screening for suitable microbial co-culture systems are still considered a promising tool for enhancing biogas production.

4.3. Anaerobic co-digestion strategy

The high carbon content in lignocellulosic wastes hinders the optimal C/N ratio required for anaerobic digestion. Therefore, it is necessary to increase the nitrogen content of lignocellulosic wastes prior to anaerobic digestion, and protein-rich wastes including food wastes and animal manures are ideal candidates to compensate for nitrogen deficiency in lignocellulosic wastes. Besides increasing the availability of feedstocks, anaerobic co-digestion (a fermentation process of two or more substrates to produce biogas) also provides the following benefits: nutrient balance (good for microbial growth); dilution of inhibitory or toxic substances (high water content in food waste or animal manure); higher load of biodegradable organic matter; and increasing methane production per unit volume [194]. Several studies have shown that methane production from lignocellulosic wastes and process performance of anaerobic digestion can be enhanced by co-digestion with various substrates. Data from the Web of Science showed that 91.8% of all publications in lignocellulosic waste co-digestion was published after 2015. Of these, animal manures were the most widely used co-substrate (38.5%), followed by food wastes (33.5%), sewage sludge (20.3%) and other co-substrates such as slaughterhouse wastes, municipal wastes and agricultural residues (7.6%).

Anaerobic digestion can be broadly classified into dry (>15% dry matter content) or wet (<15% dry matter content) processes [195]. Due to the poor fluidity and the complex structure, lignocellulosic wastes are not easily decomposed by enzymes or anaerobic microorganisms, resulting in low efficiency in practice. However, this low efficiency can be improved by adding co-substrates to improve the composition balance. Co-digestion is commonly a wet single step processes, which allows simpler mechanical handling of wastes and allows the system to be carried out in a continuous flow stirred tank reactor (CSTR) [194]. Alvarez and Liden improved methane production by wet anaerobic

co-digestion, in which livestock manure was added to quinoa stems [196]. The biodegradability of feedstocks can be enhanced by the synergistic effect of co-substrates. Wang et al. studied the effect of different mixture components of dairy manure, chicken manure and wheat straw on methane production and found that better performance of anaerobic co-digestion can be fulfilled by optimizing the feed composition and C/N ratio [197]. Similarly, the methane yield in co-digestion of cow manure and straw was significantly higher than that of mono-component anaerobic digestion [198]. Moreover, co-digestion can avoid the phenomenon of continuously increasing substrate levels during single-substrate digestion which inhibits system operation. Pages-Diaz et al. found that the anaerobic co-digestion of slaughterhouse wastes with agricultural residues did not result in the suppression of methanogenic communities compared to single digestion of slaughterhouse wastes. In the case of single digestion of slaughterhouse waste, the release of high levels of long-chain fatty acids can inhibit the fermentation process [199].

Although there are numerous reports about co-digestion of lignocellulosic material improving methane production, some studies obtained lower specific methane production during co-digestion compared to single digestion [200,201]. Since seemingly ideal co-digestion wastes also confer antagonistic effects, comprehensive and continuous experiments are recommended. It is important to characterize and evaluate the co-digestion effect before applying it to industrialization. In conclusion, anaerobic co-digestion has a positive synergistic effect on process stability and methane production, increasing the biodegradable components, facilitating contact of microorganisms or enzymes with substrates, and enriching the microbial community [194]. Successful co-digestion of lignocellulosic material with other wastes is a potentially economical process that converts lignocellulosic wastes into biogas while leaving a nutrient-rich residue that can be used as fertilizer.

4.4. Other xylophagous or saprophagous animals

Some xylophagous or saprophagous animals, like diverse taxonomic groups of insects (termites, beetles, black soldier fly etc.), earthworms and ruminant animals, also have a strong ability to degrade lignocellulosic wastes [202]. These organisms can synergistically decompose lignocellulosic biomass through a series of physiological mechanisms, including physiological mechanisms, enzymatic, and intestinal flora. Firstly, the gut or stomach of these organisms has bacteria, archaea, fungi, protozoa and different enzymatic components that efficiently digest lignocellulose. Secondly, they have specific feeding/chewing mechanisms that help physically break down lignocellulose into fine particles for subsequent adequate degradation. Finally, these organisms have developed a well-established fermentation system, and a series of inhibitory compounds produced during the fermentation process can be transferred so as not to affect the efficiency of the system.

Termites are capable of efficiently digesting lignocellulosic materials such as wood. It has been reported that there are highly expressed cellulase genes in the gut of termites [203]. In addition, genes encoding lignin-degrading enzymes and protection from reactive oxygen species and other toxic metabolites produced during lignin degradation were found in its genome [204,205]. Some xylophagous or saprophagous insects also have the potential to degrade lignocellulosic wastes. For example, Gao et al. found that black soldier flies can directly use crop straw as food [61], and some beetles have been reported to survive in wood [204]. Like termite gut microbiology, rumen microbiology has been extensively studied and applied to lignocellulosic material degradation based on its abundant internal lignocellulose degrading enzymes [206]. There is a growing interest in the use of rumen microorganisms for anaerobic digestion of lignocellulosic wastes such as crop straws [149,207], wood or sawdust [208], municipal solid waste [209]. Composting can also be used as a pretreatment before anaerobic digestion. The temperature of raw materials is increased by composting prior to biogas production, thereby reducing heat requirements for subsequent start-up of the digestion process [12].

It is worth noting that pretreatment with these macroorganisms requires an aerobic environment due to survival requirements. As Tabatabaei et al. stated microaeration pretreatment is technically more efficient and cost-effective [187]. It has long been believed that the presence of oxygen is necessary for lignin degradation, and anaerobic conditions are not conducive to lignin degradation, although the mechanism is unclear [202]. By controlling oxygen levels, providing a growth environment for many facultative bacteria, higher hydrolysis rates can be achieved to accelerate methane production [210]. On the other hand, aerobic pretreatment may lead to loss of organic matter (feeding consumption of organisms) and consequently decrease biogas yield, thus reducing oxygen content could partially avoid organic biomass loss. Last but not least, the residual oxygen in system after aerobic pretreatment does not interfere with biogas production process, as methanogens have been identified to have specific mechanisms in response to micro-aeration conditions and maintain their function with little or no inhibition [211,212].

5. Economic aspects of biogas production from lignocellulosic waste

In the economic chain of waste manipulation, many factors determine waste management costs, in which collection and transportation to processing facilities can be important factors. Lignocellulose wastes are irregular in size and difficult to store and transport, however compacting and pressing could reduce lignocellulosic waste volume and improve manipulation, leading to lower transportation costs [213]. It is difficult to put a price on the collection and transportation of MSW because of the heterogeneous and complex composition. As it is not commonly collected, forestry waste does not currently have a price in the open market. Therefore, only an estimated price could be provided, ranging from 18 to 50 UK £ per oven dry tons [214]. The characteristics of crop straw, low density and high moisture content, make their collection, transportation and storage in large quantity rather difficult. It is reported that the cost of rice straw delivered to an industrial site in Punjab is about 864.24 INR (about £9.5) per ton, including payment to farmer, baling, transportation, and storage [215]. In general, the costs mainly depend on these criteria: transport distance, storage and drying, type and size of machinery used, steepness of the terrain, and labor costs [216]. The collection and transportation of lignocellulosic waste to the biogas production plant could be economically achieved by introducing appropriate mechanization hardware and practices, in the form of larger and more efficient baling, handling, and transport equipment will result in lower costs. On the other hand, with industrialization and scale-up, biogas production plants could be set up at the source of lignocellulosic waste to significantly reduce transportation costs.

Anaerobic digestion producing biogas is one of the most promising options for lignocellulosic wastes management and valorization, as it contributes to the entire circular economy chain. It is a convenient and generally cost-effective technology that satisfies efficient disposal of waste and energy production, with possible resources recovery from digestion residues. Fig. 8 shows the pathways of biogas production from lignocellulosic wastes and its application. Part of the organic matter in industrial biogas plants remains in the solid phase of the digestate, which can be then separated and used as fertilizer [217]. Biogas generally refers to a gas mixture consisting mainly of methane (55-65%), carbon dioxide (30-35%) and other trace gases, like hydrogen sulphide [218]. Biogas from anaerobic digestion could be combusted directly for cooking or used for power generation, which emits less GHG than fossil fuels [219]. However, the presence of CO₂ in biogas limits its calorific value due to its incombustibility, thus limiting its applicability and transportability. In addition, trace amounts of H₂S could corrode equipment such as generators and diesel engines. Therefore, biogas needs to be upgraded to be used as a vehicle fuel [200], and the upgrading process generates a highly concentrated CO₂ stream



Fig. 8. Schematic diagram of biogas production pathways from lignocellulosic wastes.

leading to CO_2 capture costs as low as 20 dollars per ton [220]. Carbon prices strengthen the economic case for biogas consumption, facilitating anaerobic digestion of lignocellulosic wastes, and providing rural communities with an additional source of income.

A total of 430 biogas plants worldwide were registered with the International Energy Agency (IEA) by the end of 2015. According to EPA statistics, biogas usage will reach 14 EJ in 2050, which plays an important role in how the global energy sector can reach net-zero emissions by 2050. In addition, household and village digesters in rural areas will provide nearly 500 million households with renewable energy and clean cooking by 2030 [2]. Biogas is a consolidated market with a positive outlook, and with global policies leaning toward sustainable new energy, investment in low-carbon gases such as biogas and biomethane will rise to 14 billion dollars by 2040 [221]. For import-dependent countries, investment in biomethane supplies can replace the need for fuel imports. For example, China and India both have extensive biomethane potential, a large portion of which can be obtained at relatively low cost [59,60]. If biomethane replaces natural gas needs, the two countries would save tens of billions in import bills each year, which could help offset the cost of developing a domestic biomethane industry.

Currently, about 30 Mtoe of biomethane can be developed at a lower cost than natural gas. Methane contributes significantly to the greenhouse effect, and if policies recognize the value of avoiding methane emissions from the decomposition of feedstocks, larger biomethane production will be cost-competitive. Overall, biogas and biomethane have great economic potential in promoting the clean energy transition and achieving the sustainable development goals.

6. Perspectives and conclusions

In this review article, many biological techniques, which appear to be a promising process for the valorization of lignocellulosic wastes, are summarized. Although this review indicates that biological pretreatments are energy saving and economical, more research is still needed to address several major challenges: (1) technical challenges related to biological techniques. Anaerobic co-digestion, microbial coculture and metabolically engineered microorganisms are promising, but there are still limitations to maximize the value of lignocellulosic waste. In the future, it is possible to consider improving single step to multi-step pretreatment while integrating other advantageous technologies. (2) modification of anaerobic digestion. Based on the complex structure of lignocellulosic wastes and the instability of anaerobic digestion, it is necessary to optimize operating conditions such as temperature, pH, fermentation time, solids loading, and hydraulic retention time. On the other hand, improving anaerobic reactors by imitating AD in natural ecosystems is of interest. For example, the digestion strategies of other animal systems (e.g. rumen and termite gut) could be beneficial to the design and construction of anaerobic reactors, from simple batch reactors to complex continuous reactor systems to facilitate AD of lignocellulosic biomass. (3) kinetics and modeling studies. Understanding the fundamentals for all factors that affect the biological processes is important for improving the potential for biogas production from lignocellulosic wastes. These models can be enhanced by more experimental data and collaboration of research scholars, including evaluating the potential of different lignocellulosic wastes, developing kinetic models for lignocellulose degradation, helping to optimize the pretreatment process, describing anaerobic digestion process and finding optimal fermentation conditions.

National and regional governments have an opportunity to develop circular economy principles through the introduction of policies to support the production of biogas from lignocellulosic wastes, for example through maximizing the availability of feedstocks and supporting biogas and biomethane supply and consumption. Firstly, governments may introduce comprehensive waste management policies and regulations to strengthen the collection and classification of lignocellulosic wastes creating feedstocks for biogas production. Secondly, government should promote investment, especially in remote areas where lignocellulosic wastes are abundant, adopting strategies of distributed biogas production to avoid long-distance transportation costs to centralized large-scale biogas power plants. Finally, options include introducing usage incentives (lower usage prices) for supporting consumption, and establishing biomethane standards for injecting to the gas network and direct use as transport energy.

AD is a reliable technology for biogas production from lignocellulosic wastes, and biological techniques, which are reviewed in this article, could be vital for the valorization of lignocellulosic wastes. Using biological techniques to improve the overall efficiency of anaerobic digestion has tremendous applications for sustainability in the future. Although many biotechnologies have been highly developed, detailed experimentation is still required to optimize procedure based on kinetic models. In addition, the amount of lignocellulosic wastes generated each year is enormous, and only a small proportion is treated in a manner to reduce greenhouse gas emissions. In this regard, biogas and biomethane generated from lignocellulosic waste have great economic and environmental potential. Combined with government policy support, a system that integrates lignocellulosic wastes recycling, minimizes emissions, produces clean bioenergy, and is economically viable can be successful worldwide.

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.

Data availability

No data was used for the research described in the article.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rser.2022.112995.

Appendix A. Supplementary data

The following is the supplementary data related to this review.

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