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Review

Anaerobic Co-Digestion: A Way to Potentiate the Synergistic Effect of Multiple Substrates and Microbial Diversity

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Abstract: In this paper, the latest research in the field of anaerobic co-digestion related to the advantages of using different mixtures of substrates on the performance of the process and increasing its efficiency is reviewed. The main aspects presented in this review refer to the study of the most commonly used types of substrates, highlighting their characteristics, the diversity of microbial communities involved in the production of biogas, the applied pretreatments, and the possibility of obtaining an improved digestate as a secondary product. The main types of substrates used in anaerobic co-digestion are food waste, sewage sludge, animal manure, lignocellulosic biomass, algae, fats, oils, and greases. The data from the studied works demonstrated that the anaerobic co-digestion process improves the carbon/nitrogen ratio and nutrient balance, increases the process stability, and diminishes the concentration of toxic inhibitors. At the same time, the use of appropriate mixtures of substrates leads to an increase in the diversity of microbial communities, among which synergistic relationships are established that ultimately favor the growth of the methanogenic potential. Finally, based on the research results found, one of the main trends is the need to adapt technology to the type of substrate and the industry.

Keywords: co-digestion; digestate; microbial communities; pretreatment; perspectives; substrates

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1. Introduction

Globally, climate change represents a serious threat affecting the human factor, the environment, and the economy [1]. The use of renewable energy sources helps reduce the consumption of conventional energy, reduce greenhouse gas emissions, and thus contribute to the prevention of climate change [2]. Currently, one of the main environmental problems is the continuous increase in the amount of organic waste. Sustainable waste management, as well as the prevention and reduction of its accumulation, have become key priorities in many countries around the world [3,4].

In this context, anaerobic digestion (AD) is a key technology for the sustainable use of biomass and is being considered one of the best methods for biofuel production from biomass [5].

The AD process is considered to be at the intersection of the organic waste management sector, energy generation, food production, and land-based carbon dioxide removal [6]. Moreover, AD is promoted as an efficient method for reducing greenhouse gas emissions and improving circularity in the economy through the production of renewable energy (biogas) [6,7].

The produced biogas can be used to run micro-turbines, fuel cells, engines, and to generate heat and power [8]. Biogas can also be upgraded into biomethane by removing carbon dioxide, water vapor, and other trace gases and used in the transportation sector or pumped into the gas grid [9]. The benefits of anaerobic fermentation technology are also reflected in the stability and agronomic quality of the obtained digestate. In addition, this method of treatment is in accordance with the provisions of the European Union that assume the reduction and recovery of waste within the circular economy as well as the promotion of clean technologies [10–12].

Hydrolysis, acidogenesis, acetogenesis, and methanogenesis are the four steps in the AD of organic matter carried out by a syntrophic bacterial consortium. The bacterial consortia involved in the AD process are influenced by a number of factors, namely biodegradability, carbon/nitrogen (C/N) ratio, water content, temperature, fermentation pH value, mixing ratios, additives, toxicity, organic loading rate, and dilution ratio [13,14].

Anaerobic co-digestion (AcoD) represents the degradation process of two or more organic substrates, giving the anaerobic fermentation process a synergistic effect that leads to an increase in biogas production [11]. This process is a promising option for enhancing the yields of biogas and methane obtained from the anaerobic digestion of solid wastes [8]. It has been demonstrated that the AcoD technique is advantageous due to its enhanced methane yields, economic viability, and capacity to overcome some of the issues that arise during mono-digestion. These issues, such as unbalanced nutrients and the presence of inhibitors and recalcitrant compounds in the substrate, have made AcoD a popular field of research for improving traditional AD technology [5,15–17]. A parameter with a significant influence on the development of the AD process is the C/N ratio of the substrate. The optimum value of the used substrate is 25:1; higher C/N ratios result in lower methane concentrations in biogas, whereas substrates with a C/N ratio that is too low will lead to ammonia accumulation in the digester and inhibit methane production [3,13]. A suitable C/N ratio in the anaerobic digester can be obtained by co-digesting substrates rich in carbon, such as crop residues, with nitrogen-rich substrates, such as animal manure [17,18].

It has been shown that AcoD provides a better economic justification for installing CHP (combined heat and power) systems, which are considered the most economical method for obtaining energy from biogas [19]. AcoD improves substrate digestion and energy production by enhancing the nutrients that are available to microorganisms and the organic loading rate while decreasing the toxicity of chemical inhibitors through co-substrate dilution [20]. In Figure 1, the main advantages of AcoD technology compared with the mono-digestion process are presented.

However, the results found in the scientific literature that analyze the efficiency of the AcoD process are still insufficient. A lot of researchers conducted experiments in this field, but results varied from author to author regarding the blend proportions used in the digester. Anyway, in all the experiments, the authors reported that biogas production is enhanced by the co-digestion of different substrates. Further research in co-digestion should be completed because many types of substrates still remain unstudied.

The main aim of this article is to review the latest research in the field of AcoD related to the advantages of using different mixtures of substrates on the process performance and increasing its efficiency. The paper refers to the study of the main types of substrates, the diversity of microbial communities, applied pretreatments, and the possibility of obtaining an improved digestate as a secondary product.

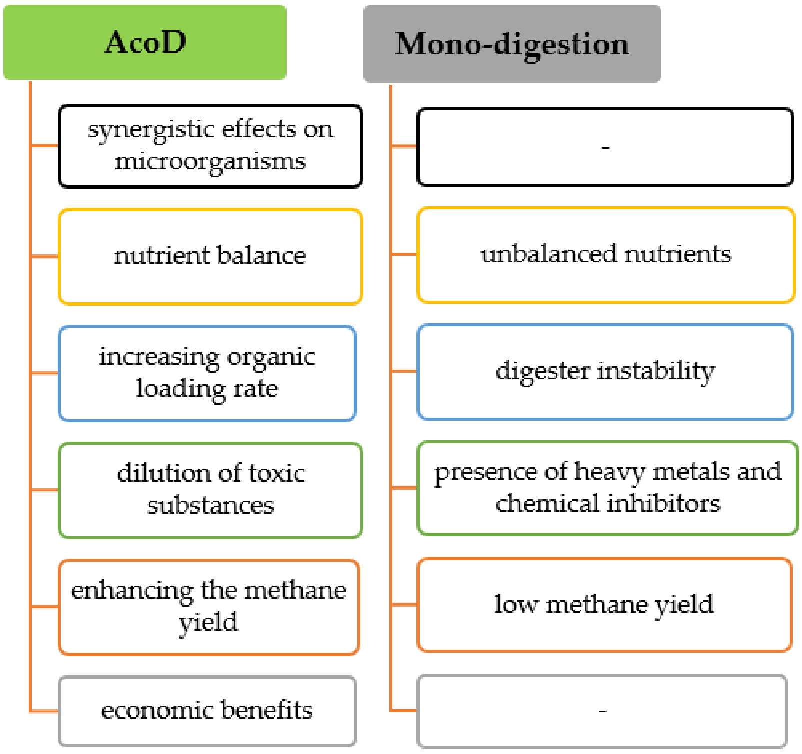

Figure 1. Advantages of AcoD technology compared with mono-digestion process (adapted from [5]).

2. Substrates Used in Co-Digestion

In the AD process, a great variety of substrates are used, each different in terms of chemical composition, water content, microbial load, presence of inhibitors, or different growth factors. The properties of the substrates depend to a great extent on the materials from which they were derived, either as by-products or as waste, on the geographical area and climate, on the applied pre-treatments, and last but not least on the socio-economic development of the region from which they come. Substrates significantly influence the yield of biogas and CH_4 due to the effect of stimulating or inhibiting the multiplication of microbial populations for certain parameters of the process. The initial composition of the substrates influences both the number, the type, and the ratio of the microbial species, their metabolic pathways, the duration of the lag phase, the generation time, and, implicitly, the growth rate. In general, the substrates used in AD are classified according to their origin or content in organic matter, although it is obvious that there will always be differences even in the case of the same type of substrate.

Since a single type of substrate with a fixed composition has a limited number of nutrients for such a large diversity of microbial populations, the use of combinations of substrates in optimal ratios ensures the stability of robust and synergistic microbiomes and provides more effectively the compounds necessary for growth and for the metabolic reactions involved in those 4 stages of AD: hydrolysis, acidogenesis, acetogenesis, and methanogenesis.

2.1. The Main Characteristics of the Substrate Used in Co-Digestion

Food waste (FW) (including FW from the industrial processing of foodstuffs as well as FW from catering, restaurants, and households), lignocellulosic materials from the agro-industrial field, forestry, parks, and gardens, animal manure, sewage sludge (SS) resulting from the aerobic treatment of wastewater, and various municipal organic solid waste, are used for the production of biogas. Each of these categories of substrates can be combined with one or more other substrates to reach an optimal C/N ratio and optimal conditions for microbial populations (Figure 2).

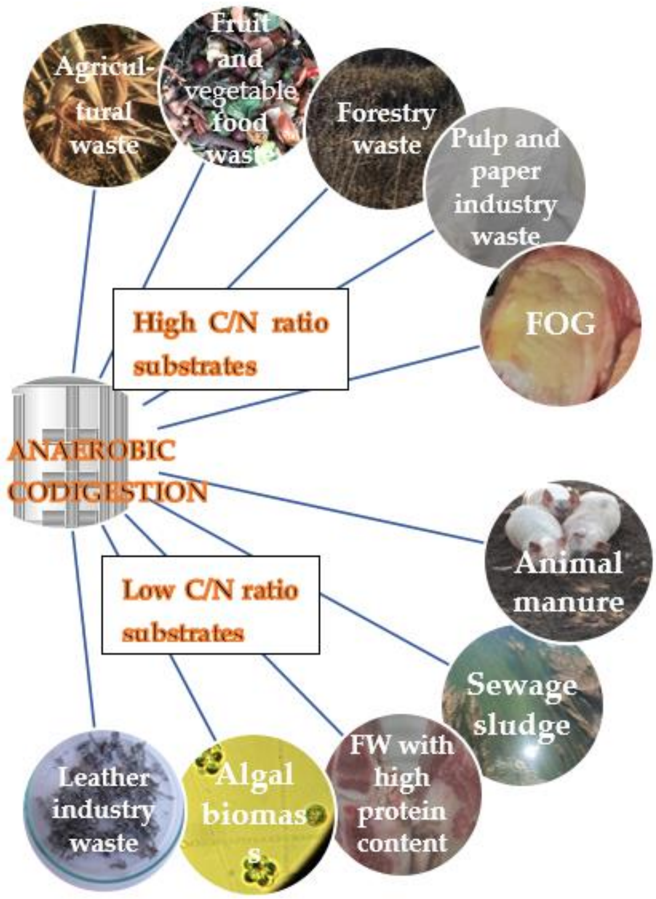

Figure 2. High and low C/N ratio substrates used in co-digestion.

SS has a high content of organic matter and an important amount of water and can be primary sludge (from the primary settler) or secondary sludge (waste-activated sludge), with a significant amount of microbial biomass. SS can contain some pathogens and various inhibitory substances for the bacteria in the AD process, such as heavy metals, antibiotics, detergents, solvents, persistent organic pollutants, etc., that can be diluted by co-digestion [21]. The mono-digestion of sludge is not effective due to the limited concentration of nutrients, low organic loading rate, difficult biodegradability, presence of extracellular polymeric substances secreted by the microorganisms [22], and harmfulness of contaminants [23–27].

Animal manure is produced in large quantities in livestock farms and is characterized by a high organic content, a low C/N ratio, and a large number of microorganisms from the digestive tract of animals [21]. Sometimes it can contain pathogenic germs that end up in the digestate. The high concentration of nitrogen compounds, especially proteins, leads to the synthesis of ammonia in the form of ammonium ions (NH_4^+) or ammonia (NH_3), which are harmful to the bacteria in the AD process and alter the balance between VFA (volatile fatty acids) and the substances in the substrate but maintain a pH suitable for methanogens. Co-digestion with appropriate substrates aims to increase the value of the C/N ratio and improve the concentration of nitrogen compounds. Usually, this type of substrate is used together with lignocellulosic materials from nearby agricultural or forestry areas to reduce costs [21,28–33].

Lignocellulosic materials have a high C/N ratio, a high carbohydrate content, and a low concentration of microelements, but their main problem is related to the availability of nutrients. Macromolecular compounds such as cellulose and lignin are difficult to transform into nutrients for bacteria and therefore generally require drastic and quite expensive pretreatments. It is obvious that this type of substrate should be mixed with substrates with a high concentration of nitrogen compounds [34–37].

FW is perhaps the most diverse and complex substrate, with properties that depend on the source of raw materials (waste from the dairy, meat and poultry, fish, fruit and vegetable, cereal and bakery, brewing, and winery industries, among others). FW has an increased biodegradability due to the high content of organic compounds (carbohydrate: 12–74%, protein: 14–18%, lipid: 4–34%, and dry weight) [38].

In the case of FW, both the water content varies (minimum, for example, for residues from the milling industry and higher for waste from fruit and vegetable processing, dairy industry) as well as the C/N ratio, which can be high in waste from the processing industry (fruits and vegetables) or small in residues from the dairy industry, meat and poultry, and fish. These types of substrates are rich in nutrients that are generally easily available to microbial populations, growth factors (amino acids, purines and pyrimidines, vitamins), and macro- and micronutrients. FW can have a variable microbial load, high, for example, for waste from the fermentation industry (whey) or processes that use starter cultures. It may contain traces of various food additives, of which preservatives in relatively large quantities could influence the viability of AD bacteria. FW also differs depending on its source: industrial, household, or public food production, but also depending on regional, seasonal, and socio-cultural characteristics [38–41].

A special problem is the presence in FW and sewers of vegetable and animal fats from slaughterhouses or the extractive industry of vegetable oils, but also from restaurants, fast food outlets, and households. These fats, called FOG (fats, oils, and greases), once they reach the sewers, can restrict the flow and even clog the pipes [42]. The fats present in the substrate of the AD process are hydrolyzed by lipolytic microorganisms into glycerol and long-chain fatty acids, which are then transformed into acetate and formate/hydrogen by acetogenic bacteria and then into methane by methanogenic archaea [43]. Furthermore, water from slaughterhouses has a high concentration of fats and proteins dissolved or in suspension, contributing to improving the composition of the substrate in co-digestion and increasing the pH value and the content of nitrogen and micronutrients [44].

Other sources of organic matter, used less often as a substrate in AcoD, are waste from the leather industry, textile dyeing sludge, the pulp and paper industry, and others, which generate different residues depending on the raw material processed. In general, these substrates are characterized by their limited composition in nutrients, but also by the presence of inhibitors used as specific process additives. The proteinaceous waste resulting from the leather industry is difficult to degrade and often contains chromium, which is toxic to the bacterial cell (for example, “chrome shavings” resulting from hide shaving operations) [45,46].

The pulp and paper industry generates recalcitrant lignocellulosic materials, which slow down the rate of degradation of the substrate, along with paper-making fillers such as kaolin and calcium carbonate, pitch, lignin secondary products, and ash [47–49].

Micro- and macroalgae have the ability to grow in different types of wastewaters, such as municipal, livestock farming, food processing, and agriculture runoff wastewater [50–54]. In addition, under favorable conditions, algae can produce harmful algal blooms, which can severely affect the environment, especially the water biocenosis in coastal areas [55], and also the tourism economy. Algal biomass is characterized by low C/N ratio values, which are in the range of 4–10 [56], causing the release of toxic ammonia for methanogens. On the other hand, algae are rich in nutrients and minerals that improve the growth of bacterial cells [57]. Although relatively few studies are reported, algae are used in co-digestion processes with other substrates such as animal manure, SS, FW, or others with a high C content to balance the C/N ratio [58–60].

In most studies to date, FW has been used in the co-digestion process together with the following substrates: SS [24–27,39,57,61–68], cattle rumen content [69], dairy manure [70–73], chicken manure [74], dry fallen leaves and cow dung [75], human feces and toilet paper [76], solid leachate [77], yard waste [78], straw [79,80], mixed microalgae [81], *Spirulina platensis* alga [52], olive milling waste [81], FOG [82], textile dyeing sludge [45], petroleum oil sludge [83], biochar [84], but also in other mixtures.

The lignocellulosic materials in co-digestion are characterized by a poor buffering capacity and an unbalanced C/N ratio and can be introduced into mixtures that contain: different organic wastes, such as SS, dairy manure, fruit wastes, brewery trub and slaughterhouse [34], cattle dung [35], tomato residues and dairy manure [85], cucumber residue and pig manure [86], pig manure and sludge [87], FW [88], and chicken manure [89,90].

SS was used in a mixture with FW [24,25,27,39,57,61,62,65–68], fruit and vegetable waste [26], coffee pulp, cattle manure and FW [91], chicken manure [23], pig manure [92], yard waste [78], agricultural residues (wine vinasse and poultry manure) [93], different selected organic fractions of municipal solid waste [64], citrus peel wastes and biochar [94], olive waste [95], fatty wastewater [96], FOG [42,97], algae, and FW [52].

The biogas yield is the most significant quantity that shows how efficient an AcoD process is, as can be seen in Table 1. From different studies, the methane yield value was in the range of 50–600 mL CH_4/gVS, with maximum values for mixtures of FW and SS, FW and brown water, or municipal solid waste and SS. The presented data are valid for the digestion conditions of each experiment (temperature, C/N ratio, volume, and type of reactor) and are thus not fully conclusive for a certain mixture of substrates.

Table 1. Methane yield, C/N ratio and digester type for different substrate mixtures in AcoD.

Substrate	Methane Yield (mL CH_4/gVS$_{added}$)	C/N	Hydraulic Retention Time (Days)	Temperature (°C)	Digester Type/Volume (mL)	Reference
			Low C/N ratio substrates			
FW and waste-activated sludge	407	/	302	35–55	high frequency feeding system, 3000	[98]
FW and SS	/	11–17	15–30	37	/	[99]
FW and SS	305.4	14.5	-	35	high-solid anaerobic membrane bioreactor, 15,000	[61]
FW, cattle manure and corn straw	500	13–43	25	37 ± 2	long-term semi-continuous AcoD, 300	[80]
FW, newsprint paper, and branches	129.7–534.4	/	30	37	batch culture system, 400	[100]
FW and brown water	728	/	15–20	37	two-stage AcoD, 10,000–35,000	[101]
FW and SS	0.29 L CH_4/g COD removed	10.8–38.8	70–180	37	simulation model	[102]
SS with crude or pretreated glycerol	45	6.42	15–30	30	three stages, 100	[103]
Excess sludge with chicken manure	82.4–123.1	/	40	37–55	batch system, glass digester	[23]
SS and glycerol	370–483	/	45	37 ± 1	continuous operation 160	[104]
Municipal solid waste and SS	571–675	10.59–31.35	30	37	glass bottles, 100	[64]
Palm oil mill effluent with decanter cake	515	10.7–15.8	35	37 ± 1	graduated cylinder, 250	[105]
Dark fermentation of SS and agricultural residues	52.05	14.24	20	35	amber batch type flasks, 120	[93]
Cheese whey and septage	342.22	34.01	35	35	glass flasks, 100	[106]
Fresh vinegar residue and pig manure	233.77	14.5–24.4	20	35 ± 2	semi-continuous stirred tank reactor, 70,000	[107]
Taihu blue algae with swine manure	212.7	5.8–11.41	22	37	400	[108]
Diary processing waste	178.1	/	3–15	37–58	two-stage digestion in induced bed reactors, 60,000	[109]
Leather waste with raw and wheat straw	43.15	10.88–68.87	274	35	Hermetically sealed bench scale bioreactors, built in cylindrical glasses, 300	[46]
Mixed microalgae and FW	639.8 ± 1.3	15.43	40	35	120	[110]

Table 1. *Cont.*

Substrate	Methane Yield (mL CH_4/gVS_{added})	C/N	Hydraulic Retention Time (Days)	Temperature (°C)	Digester Type/Volume (mL)	Reference
Decanter cake and empty fruit bunch	257	9.72–49.55	35	35	batch reactors, 250	[111]
Rice wastewater with cow dung slurry	292	23.717	4	37 ± 2	two-stage, 250–500	[112]
Press mud and bagasse from sugar mill	450	13	35	35–37	glass flasks, 1000	[113]
Sargassum-pig manure	441.47	16.8	100	37 ± 1	serum bottles, 305	[60]
Wastewater grown algae-bacteria polyculture biomass and cellulose	323–380	5.67	60	35 ± 0.5	serum bottles, 150	[50]
High C/N ratio substrates						
Banana stem and swine manure	357.9	/	40	35 ± 1	solid state, 1000	[28]
Corn stover: Swine manure	281	25	21	37 ± 1	8000	[114]
Wheat straw with cattle manure	254.6	16.6–88.1	35	37 ± 1	1000	[115]
Lignocellulosic feedstock	320–360	/	40	28–32	1000	[35]
NaOH-treated biphasic olives with FW	503.6	/	30	37	stirred tank reactor, 6000	[81]
Rice straw and pig manure	235.81	35–38	190	37–55	two reactors of temperature phased AcoD 1000–8000	[116]
Mango and microalgal residue biomass	204.4	/	30	37	glass bottle equipped with septum cap, 250	[58]

2.2. Factors Influencing the Co-Digestion Process

The major important factors in the co-digestion process are both the composition of the substrate resulting from various blending of organic waste and their mixing ratio, as well as the pretreatments applied, the system temperature (under mesophilic or thermophilic conditions), the type and quantity of the inoculum, the type and operating mode of the reactor (batch or continuous, one-stage, two-stage, or multiple-stage reactors, anaerobic membrane bioreactor), the presence of inhibitors, and others.

The stability of the process depends to a significant extent on the values of pH, ammonia, and VFAs [41]. Studies have shown that the activity of methanogenic bacteria is optimal at pH values between 6.5 and 7.5 [117]. Proteins and other nitrogen-containing compounds produce ammonia nitrogen through degradation, which, in appropriate quantities, maintains the pH range within favorable limits for methanogens but, in high concentrations (greater than 700 mg/L), act by inhibiting methanogenesis [27,109,118]. Furthermore, the concentration of VFAs in the reactor must have values that allow for maintaining an optimal pH of approximately 1300 mg/L TVFA (total volatile fatty acids) [41]. Substrates with high C/N ratios produce high concentrations of VFA, and therefore should be mixed with nitrogenous feedstock such as animal manure or protein FW from the meat or fish industry.

The inoculation of the biogas reactor must be carried out in such a way as to ensure the density of the microbial population necessary to start the process. The lag phase that usually occurs due to the adaptation time of the microorganisms to the new conditions in the reactor should be minimal, and the conditions should allow for the optimal multiplication of the species. The use of an inoculum resulting from the previous series of the anaerobic digestion process or of some substrates with a large number and diversity of microorganisms, for example, cattle rumen content [69], leads to the start and normal development of the stages of the process (hydrolysis, acidogenesis, acetogenesis, and methanogenesis). However, one of the goals of co-digestion is to prolong the degradation time of organic compounds, decrease the hydrolysis rate, and in this way improve the stability of the process [41].

The diversity of microbial communities in the hydrolysis stage of the co-digestion process is positively influenced by the blending of substrates, and, moreover, the depolymerizing activity of exoenzymes increases the amount of soluble oligo- and monomeric compounds in the reactor. These nutrients, in their turn, favor the balance and stability of the system through their greater variety and improve cooperative relations and the synergistic effect in the following stages of acidogenesis and acetogenesis. Co-digestion also improves and balances the syntrophic relationship between acidogenic and methanogenic bacteria by creating favorable conditions for archaeal communities. In addition, the efficiency of AcoD increases significantly through different pretreatment methods, especially for lignocellulosic material, and is influenced by pH, VFA, Eh, organic loading, temperature, and others.

3. Microbial Communities in AcoD

Considering synergism as a cooperative relationship in which the associated species have an effect that each of them could not achieve individually, in the AcoD process, each bacterium synthesizes and releases into the environment important quantities of the nutrients needed by the others in such a way that they meet each other's growth needs.

The communities of microorganisms in the digester are complex and mostly composed of bacteria, which are different depending on the nature of the waste. The facultative anaerobes have the role of consuming and depleting the small amounts of oxygen present in the environment and of modifying the potential Eh to a level accessible to the obligate anaerobic microorganisms, which, over time, become the predominantly active population in the digester.

The study of microbial communities became possible after the discovery of advanced molecular biology techniques, among which are PCR (Polymerase Chain Reaction), cloning, and sequencing of marker genes, molecular fingerprinting (terminal restriction fragment length polymorphism (T-RFLP), single-strand conformation polymorphism (SSCP), denaturing gradient gel electrophoresis (DGGE), and automated ribosomal intergenic spacer analysis (ARISA)), quantification of individual taxa of microorganisms using quantitative PCR (qPCR) and droplet digital PCR, Fluorescent in Situ Hybridization (FISH), microarrays, others.

In the first stage, hydrolysis, the degradation of complex organic substances, such as those of vegetable origin (cellulose, lignin, etc.), is facilitated by the mixture of two or three substrates, each with different communities of microorganisms [29]. Most hydrolytic microorganisms come from the multiplication of microbial populations from the initial substrates or from the inoculum.

In hydrolysis reactions, macromolecular organic compounds are released as different monomers or oligomers: glucose and cellobiose from cellulose, glucose and maltose from starch, xylose from hemicellulose, amino acids from proteins, and long-chain fatty acids (LCFA) and glycerol from lipids. Figure 3 shows the main hydrolytic enzymes involved in substrate degradation and the appearance of the producing colonies grown on specific culture media. The most important hydrolytic bacteria belong to the phyla *Firmicutes* and *Bacteroides*, among others.

In the acidogenesis stage, the products released from the hydrolysis reactions are transformed by fermentation into short-chain fatty acids such as acetate, propionate, butyrate, valerate, and isobutyrate by acidogens. The main acidogenic bacteria belong to the phyla *Firmicutes*, *Bacteroidetes*, *Chloroflexi*, *Proteobacteria*, and *Atribacteria*.

Acetate, formate, H_2, and CO_2, resulting from acidogenesis, are directly utilized by methanogens for biogas synthesis. In this stage, medium-chain fatty acids (MCFA) and long-chain fatty acids (LCFA) from lipid hydrolysis are also produced. These compounds will be oxidized to acetate, H_2, and CO_2 through syntrophic acetogenesis. Hydrogenotrophic methanogenic bacteria live in proximity to syntrophic acetogens and consume the H_2 released from the syntrophic bacteria. The activity of syntrophic acetogens is indispensable for maintaining a stable and robust process and for reducing the production of inhibitory compounds such as propionate, for example.

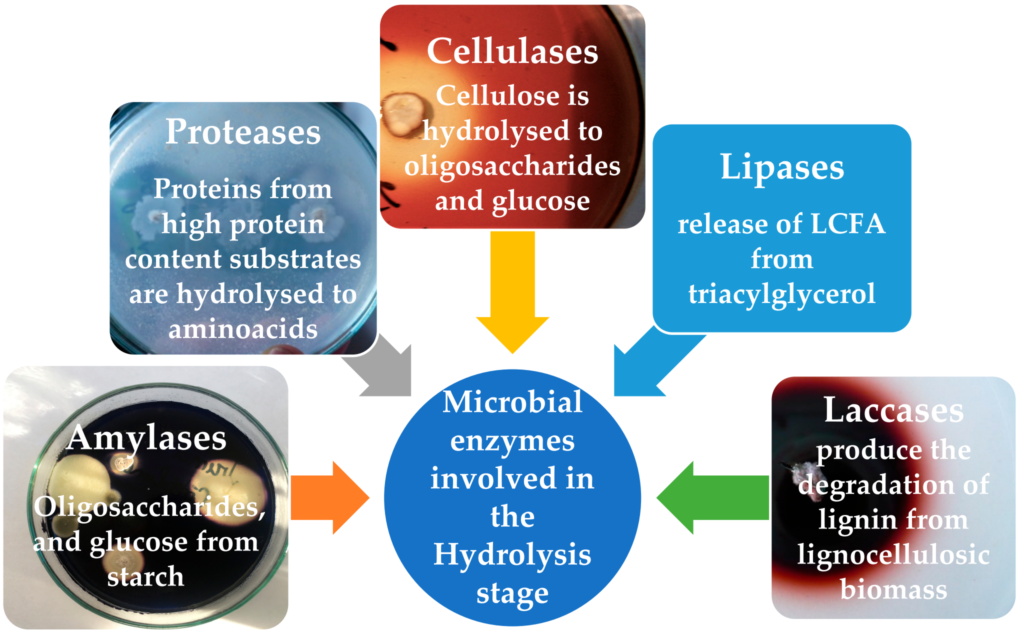

Figure 3. Amylases, proteases, cellulases, lipases, and laccases are produced by microorganisms in the hydrolysis stage of AcoD.

The methanogens can be classified into three groups depending on the substrate and the metabolic pathway used: (a) acetotrophic or acetoclastic methanogens, (use acetate to produce methane); (b) hydrogenotrophic methanogens, (use formate and H_2 to reduce CO_2 to CH_4); and (c) methylotrophic methanogens, (produce CH_4 from methyl compounds). The main methanogenic hydrogenotrophic archaea belong to the genera *Methanoculleus*, *Methanobacterium*, *Methanobrevibacter*, *Methanospirillum*, and *Methanothermobacter*. Acetotrophic methanogens are represented by *Methanosaeta* and *Methanosarcina*.

In 2022, Liu et al. [31] showed that in AcoD of Chinese cabbage waste and cow manure at mesophilic and thermophilic temperatures, the dominant bacterial communities at mesophilic temperatures are *Firmicutes* (30.3–44.3%), *Bacteroidetes* (36.1–47.9%), *Synergistetes* (2.6–15.2%), *Actinobacteria* (0.1–2.3%), *Cloacimonetes* (0.01–6.73%), and *Spirochaetes* (0.03–3.51%). The most active microorganisms producing proteolytic and cellulolytic enzymes [119] belong to *Firmicutes* and *Bacteroidetes*. The dominant thermophilic bacterial populations under temperature conditions of 55 °C were *Firmicutes* (60.2–83.5%), *Thermotogae* (0.2–31.2%), *Actinobacteria* (0.1–6.8%), and *Proteobacteria* (0.1–2.2%). At 37 °C, the archaeal bacteria are *Methanosarcina* (4.5–29.4%), *Methanofollis* (1.4–41.5%), *Methanoculleus* (0.8–11.0%), *Methanocorpusculum* (0.2–51.7%), and *Methanobacterium* (1.1–10.1%). At higher temperatures, *Methanosarcina* (16.8–54.0%), *Methanothermobacter* (0.5–26.5%), and *Methanoculleus* (0.2–28.4%) are predominant. Therefore, the type and number of microorganisms in the co-digestion process are closely related to the composition of the substrate and the temperature in the digester.

A similar study was carried out by Wang et al. in 2022 [23] about the AcoD of excess sludge with chicken manure. Wang finds that the main thermophilic non-methanogenic bacteria belong to *Firmicutes* (26.4–37.6%), *Actinobacteria* (13.5–29.1%), *Proteobacteria* (5.2–15.7%), *Chloroflexi* (3.5–15.0%), *Thermotogae* (0.6–6.7%), and *Synergistetes*. Among the mesophilic communities in the reactor, the most important were *Firmicutes* (2.2–9.9%), *Actinobacteria* (9.8–19.2%), *Proteobacteria* (11.1–25.4%), *Chloroflexi* (20.1–36.4%), *Bacteroidetes* (3.2–9.1%), *Synergistetes* (3.6–9.5%), *Acidobacteria* (0.5–3.4%), *Planctomycetes* (1.5–2.6%), and *Spirochaetes* (0.5–1.5%). The authors also found differences in the structure of the archaea community as follows: at thermophilic temperatures, *Methanosaeta* (2.7–5.9%), *Methanospirillum* (0.8–1.9%) and *Methanosarcina* (13.2–59.5%) are dominant, while at mesophilic temperatures, predominate *Methanosaeta* (57.1–84.2%), *Methanobacterium* (5.0–12.9%), *Methanospirillum* (3.7–9.0%), *Methanolinea* (0.4–5.9%) and *Methanobrevibacter* (0.5–2.1%).

Studying the microbial populations in AcoD of chicken manure and cardboard, Zhao et al. in 2021 [29] found that the main hydrolytic bacteria in anaerobic conditions belong to the phylum *Firmicutes*, *Bacteroidetes*, *Fibrobacter*, *Spirochaetes*, and *Thermotogae* [120]. Among the dominant bacteria, *Proteobacteria* could degrade glucose, propionate, butyrate, and acetate [121]. Zhao et al. in 2021 [29] found that increasing the percentage of cardboard waste in the mixture with chicken manure leads to an increase in the abundance of the *Proteobacteria*. The Gram-negative bacteria from the *Proteobacteria* group are able to degrade organic compounds in cardboard and have a high activity for glucose, propionate, butyrate, and acetate degradation [29]. In the methanogenesis stage, the authors [29] demonstrated that the dominant methanogens were *Methanosaeta*, *Methanobacterium*, *Methanolinea*, and *Methanomassiliicoccus*, and the structure of the archaeal communities is strongly influenced by the composition of the substrate.

Li et al. [30] showed that in a batch experiment using chicken manure (CM) and microalgae *Chlorella* sp. as co-substrates, *Methanosaeta* and *Methanosarcina* were the dominant methanogens in all stages, and the hydrogenotrophic methanogens *Methanospirillum* and *Methanobacterium* were the two other main genera since the 15th day [30].

The major influence of the inoculum was demonstrated in the process of co-digestion of organic fractions of municipal solid waste by Zhou et al. in 2021 [100,122]. The structure of the microbial populations was analyzed by PCR amplification and high-throughput 16S rRNA gene sequencing.

The most important groups of bacteria were *Firmicutes* and *Bacteroidetes*, in which the dominant orders were *Clostridiales*, *Thermoanaerobacterales*, and *Sphingobacteriales*, involved in the hydrolytic degradation of the polymer components in the substrate as well as in the acidogenesis and acetogenesis processes. The majority of methanogenic bacteria belonged to the orders *Methanobacteriales*, *Methanocellales*, *Methanomicrobiales*, *Methanococcales*, *Methanopyrales*, and *Methanosarcinales*.

In 2022, Adarme et al. [123] studied the co-digestion of sugarcane biorefinery byproducts in single- and two-stage systems using hemicelluloses hydrolysate, vinasse, yeast extract, and sugarcane bagasse fly ashes. Using PCR amplification and Illumina technology, the authors demonstrated that the majority of bacteria belong to the genera *Clostridium* (62.8%), *Bacteroides* (11.3%), *Desulfovibrio* (19.1%), *Lactobacillus* (67.7%), *Lactococcus* (22.5%), *Longilinea* (78%), *Methanosaeta* (19.2%), and *Syntrophus* (18.9%), which are related to process parameters.

In a mixture of green waste, *Enteromorpha*, and chicken manure, Zhao et al., in 2022 [55], found that the dominant bacteria belong to the phyla *Bacteroidetes*, *Synergistetes*, *Firmicutes*, and *Chloroflexi*, which represent approximately 80% of the total microbial populations. Bacteria from the *Firmicutes* group synthesized hydrolytic enzymes from the class of cellulases and proteases with degradative action on the substrate, while the *Synergistetes* group synthesized acetate and hydrogen that will be used by methanogenic archaea. The authors noted the abundance of syntrophic VFA-oxidizing acetogens such as *Syntrophomonas* and *Syntrophobacter* in the co-digestion process.

Xing et al., 2022 [65] analyzed the structure of the communities of microorganisms in the co-digestion process of waste activated sludge and FW and showed that *Bacteroidetes*, *Spirochaetes*, *Firmicutes*, *Chloroflexi*, and *Synergistetes* are the dominant bacteria. *Methanothrix*, *Methanosaeta*, and *Methanosarcina* are present among the methanogens.

A particular case of obtaining biogas through the AcoD of fats, oils, and grease with municipal sludge. For this mixture of substrates, Ziels et al., in 2016 [43], studied syntrophic LCFA-degrading bacteria using qPCR analysis. In substrates with high fat content, such as slaughterhouse waste or from the oil industry, LCFA are formed by hydrolysis of fats, which require the action of proton-reducing acetogenic bacteria that convert LCFA into acetate and formate/hydrogen. Bacteria with this ability are part of the families *Syntrophomonadaceae* and *Syntrophaceae*. Studies have shown that LCFA conversion to methane is the rate-limiting step for fat utilization in AD. From the archaea community, the most representative groups were *Methanospirillum* and *Methanosaeta* species in a syntrophic relationship with the *Syntrophomonas* genus. Based on the research data from recent years, Figure 4 shows the main phyla and orders of bacteria in the four stages of anaerobic digestion.

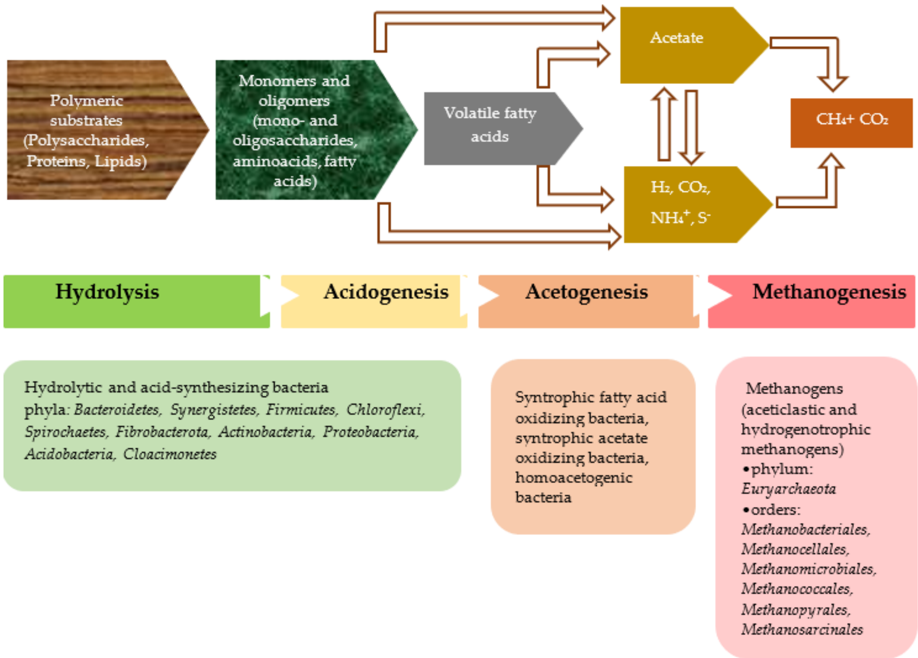

Figure 4. The main taxa of bacteria in the four stages of anaerobic digestion.

Using FISH analysis, Montecchio et al. in 2019 [24] suggest that waste-activated sludge, when used in co-digestion with FW, improves the methanogenic activity and also has the capacity to buffer the acids resulting from the acidogenesis stage. They showed that the abundance of methanogens is approximately 30% of the total microbial population, and the remaining 70% are fermentative bacteria.

4. AcoD Pretreatments

AcoD pretreatment is primarily used to increase the substrate's capacity for biodegradation and speed up the digestive process. Pretreatment techniques come in a variety of forms, including mechanical, thermal, biological, and chemical ones. The choice of method will depend on the kind of substrate being used and the desired result of the procedure. Each method has advantages and cons of its own. There have been studies completed that consider many inputs and outputs of the process. These pretreatments could potentially increase methane generation and waste management; however, their use must first be shown to be economically feasible given the higher operational cost.

1. Physical pretreatment: to promote AcoD and decrease the influence of particle size substrate, some researchers in the literature suggest using mechanical techniques [124]. This pretreatment aids in increasing surface area by breaking the polymeric chains and decreasing the particle size, which also helps with hydrolysis. Usually, physical techniques do not generate any hazardous elements, making them safe for the environment [125]. According to scientists the disadvantage that highly influences the decision to use physical pretreatment is related to energy consumption, which can be influenced by the desired particle size [126,127]. The variables that influence the results of the pretreatment are substrate type (feedstock), temperature, pressure, and retention time. Thus, the overall results expressed that the best method for mechanical pretreatment appears to depend on the diversity of materials and cannot

be recommended as a universal strategy, according to the observed variances in the impacts of particle size, time, and grinding velocity [126,128–132].

2. Chemical pretreatment: one of the most efficient approaches involves chemical pretreatments with acids, alkalis, and organic solvents [133], as they can be quite good at dissolving more intricately structured substrates. For example, for lignocellulosic biomass, this process further enhances the bioavailability of carbohydrates by removing lignin and/or lowering the degree of polymerization and cellulose crystallinity [134]. Since it is frequently less expensive, results in faster rates of degradation, and has superior efficacy for complex organic compounds, chemical pretreatment has attracted more attention [135]. One of the most popular kinds of chemical pretreatment is acid hydrolysis, which uses diluted acids such as sulfuric acid or hydrochloric acid [136–138]. Another often-used method is called alkaline pretreatment, and it breaks down the lignin and hemicellulose. Ionic liquid pretreatment is a relatively recent technique but widely spread [139,140]. Since ionic liquids may be recycled and reused, this procedure is regarded as more environmentally friendly than acid or alkaline treatments [140,141]. Mechanical, physical, and organosolv procedures are some other chemical pretreatment methods; each has advantages and disadvantages of its own. The particular substrate, the desired outcome, the equipment and facilities available, as well as other factors, all have an impact on the pretreatment method selection. Chemical pretreatment is a difficult procedure that must carefully take into account the particular substrate, the anticipated end product, and the accessibility of tools and resources, among other things [142].
3. Thermal pretreatments—These represent a common technique for different types of substrates. For example, if lignocellulosic substrates areused to make the sugars more accessible for fermentation or other downstream processing, the materials are subjected to a procedure called heat pretreatment [143]. Thermal pretreatment's primary objective is the removal of lignin and hemicellulose, which pose the most challenges to the effective hydrolysis of cellulose. Steam explosion, which uses high-pressure steam to rapidly heat and then rapidly cool the substrate, is one of the most popular thermal pretreatment techniques [144]. Consequently, the separation of cellulose, hemicellulose, and lignin makes it easier to access the sugars for fermentation. Some techniques for thermal pretreatment employ high temperatures and a small amount of water to break down the lignin and hemicellulose. Given that it requires less energy and produces less waste than a steam explosion, this method is thought to be more eco-friendly [145]. Thermal pretreatment is also frequently used to treat raw or processed sludge, which improves dewatering, solubility, viscosity, and results in fewer pathogenic bacteria. This is because the non-soluble fraction's structure is changed by the heat treatment, making it simpler for microbes to break it down [146]. Ultrasonication, microwave, pyrolysis, ohmic heating (OH), and microwave-assisted thermal pretreatment are further thermal pretreatment techniques [147]. Each has pros and cons. The unique substrate, the desired end product, and the equipment and facilities available all play a role in the pretreatment method selection. Overall, the transformation of lignocellulosic substrates into valuable products, including biofuels, chemicals, and materials, requires thermal pretreatment. It is a complicated procedure that calls for careful thought about the particular substrate and the desired end result, as well as the accessibility of tools and resources.
4. Combined pretreatments—Research has demonstrated that combining two pretreatments, such as biological pretreatment with chemical or physical techniques, is considerably more effective than employing a chemical or biological approach alone [148]. For example, it has been demonstrated that the use of fungal pretreatment for the commercialization price of methane has been deemed impracticable due to the low hydrolysis rate and the slow processing speed of the procedure. However, the efficiency and profitability of the overall process are boosted when paired with a mechanical or chemical pretreatment [149]. Furthermore, according to ref. [150], to increase produc-

tivity, mechanical pretreatment is frequently followed by chemical, physicochemical, or biological pretreatment.

5. AcoD Management of Digestate

AcoD, the simultaneous digestion of two or more feedstocks, offers a chance to overcome the limitations of mono-digestion. Co-substrate addition can have a positive or negative effect on the AcoD process as well as digestate and biogas processing afterward. The biogas and digestate represent the main end products of anaerobic digestion/co-digestion [151].

One of the main advantages of co-digestion is the production of safe and superior-quality co-digestate for agricultural use [152]. Additionally, the co-digestate presents a higher bioavailability of nutrients when it is utilized for composting, vermicomposting (converting organic waste into fertilizer using earthworms), mushroom farming, and black soldier fly (a valuable insect species whose larvae have enormous potential for converting organic waste into compost) growing [38].

Through anaerobic digestion, the complex organic compounds present in the feedstocks are converted into plant nutrients if the digestate is utilized in agriculture. But, the use of mono-digestate obtained from feedstocks such as SS or animal manure causes a number of environmental issues, such as the increase of soil salinity, ecotoxicity, and phytotoxicity, or the accumulation of heavy metals. As a conclusion of various research studies, it was observed that co-digestion can solve these issues [153–155]. Montoro et al. [156] showed in their study that the co-digestion of dairy cattle manure with sweet potatoes (minimum 30%) led to a higher concentration of N and K (22.9% and 8.3%) in the co-digestate, compared with the results obtained in the case of anaerobic digestion of cattle manure (13.5% K and 5.8% N). Another study conducted by Kataki et al. [154] concluded that the digestate concentration of nutrients (Ca, Cu, S, Mo, Ni, Zn, and Mn) was higher in the case of co-digestion compared with mono-digestion. Wang et al. [157] studied the co-digestion of acorn slag waste with dairy manure, and they obtained a 7.4% (w/w) total nutrient content (total N, total K, and total P summation), which was higher than the results obtained from individual feedstock mono-digestion. Experiments made by Herrmann et al. [158] showed that anaerobic digestates produced by the co-digestion of animal slurries and maize ensilage present a 30% higher nitrogen fertilizer value compared with the value obtained for cattle and pig slurries. During the co-digestion of microalgal residues with waste activated sludge, a higher nutrient availability (NH_3, total phosphorus, and total nitrogen) compared with mono-digestion of microalgal biomass was observed. This conclusion was confirmed by the wheat growth, which had a higher value (62.5% dry weight basis) [159]. The same trend was observed by Iocoli et al. [160] in their research. The co-digestate obtained from cattle manure with onion residue co-digestion provided a higher coverage area of 47.8% for *Latuca sativa* (L.) compared with the digestate of cattle manure.

It is important to mention that using digestate in excess or applying it repeatedly might cause an increase in salinity and inhibition of plant growth, meaning an increase in phytotoxicity [152]. Furthermore, it is crucial to understand how nutrients from various substrates are balanced when co-digestion is used. It's important to consider the potential for secondary pollution when too many fertilizers are applied to the land [161]. If incorrectly exposed to agricultural land, some digestates with high concentrations of ammonium, salt, COD, phosphate, and color represent a serious risk to the environment and all organisms [162]. Astals et al. [163] concluded that the digestate obtained from the co-digestion of pig manure with crude glycerol cannot be used directly as soil fertilizer or conditioner. This is the consequence of the high levels of biodegradable matter present in the digestate, which can have a negative impact on the soil or plant. Additionally, if animal waste such as manure is used in the co-digestion, a hygenisation process must be carried out to minimize the spread of unwanted materials when digestate is spread on land [164].

5.1. Digestate Dewaterability

Digestate is primarily composed of water, with only 5–10% of it being solids. Dewatering of the digestate, which represents a solid/liquid separation, is therefore a crucial step in order to save transportation costs and ensure efficient digestate management [151].

The enhancement of digestate dewaterability by co-digestion was reported in the specialty literature. Thus, Levia et al. [165] observed the improvement of digestate dewaterability during the AcoD of fruit-juice/wine production waste with leachate from municipal sludge cake; the co-digestion also reduced the pathogen density. Dennehy et al. [166] showed in their study that the digestate's dewaterability is significantly enhanced with the decrease in retention time for FW and pig manure co-digestion. A positive correlation was observed between the volatile solids content and the digestate dewaterability from SS [167].

The digestate dewatering consists of a polymer addition process and a physical separation method. The polymer addition process reduces the specific resistance to filtration, thus the digestate dewaterability being improved. For the physical separation (dewatering) of the digestate, different types of equipment can be used, such as centrifuges, screw presses, or belt presses [151]. At the FW co-digestion, Higging et al. [168] observed that the increase in polymer demand led to improved digestate dewaterability, quantified by the increase in final solid cake content.

5.2. Liquid Fraction of Digestate

The liquid fraction of digestate (LFD), also called filtrate or sludge centrate, from the dewatering of digestate resulted in co-digestion with a protein-rich co-substrate (such as FW) and presents a higher content of nitrogen and phosphorus than mono-digestion. In the co-digestion of dairy manure with crude glycerol and bone meal, an important increase in NH_3-N when compared with dairy manure mono-digestion was observed [169].

Carlos-Pinedo et al. [161] observed that the liquid fraction of digestate obtained from AcoD of a mixture of substrates (biowaste, horse manure, and wood chips) presented the highest nutrient content (especially in phosphorus and total carbon-biological). An important step is the recovery of nutrients present in LFD in order to decrease the obstruction caused by struvite (a crystalline mineral composed of equimolar concentrations of magnesium, ammonium, and phosphate), eliminate the phosphorus, and ensure a sustainable fertilizer source [151].

The LFD from co-digestion of FW, swine manure, and maize silage can successfully replace synthetic N fertilizer without maize yield losses and with important ecological benefits for the soil, especially [170]. Muscolo et al. [171] observed an improvement in soil fertility, meaning the soil chemistry and bioconversion, when LFD obtained from citrus pulp and olive waste with animal manure co-digestion was applied.

Due to the high nutrient content and low content in suspended solids, the LFD is recommended as a culture medium for the growth of both micro- and macro-algae. Furthermore, the LFD with high nutrients content can be utilized for the cultivation of fruits and vegetables via bioponics [172].

5.3. Solid Fraction of Digestate

The anaerobic digestion of feedstocks with high Ca content, such as compost of household waste and municipal solid waste compost, gives a mono-digestate with increased amorphous Ca-P compounds, thus limiting the availability of P for plant nutrition [173]. Another study concluded that the mono-digestate obtained from agricultural residues contains recalcitrant organic matter, which contributes to a higher humification index [154]. Thus, it is necessary to reduce the phytotoxicity and ensure the nutrient equilibrium of feedstocks via co-digestion. The digestates solid fractions are usually utilized for land application as organic fertilizer. In order to enhance their quality, the co-digestates solid fraction may be composted or co-composted [174,175]. Additionally, stabilization through vermicomposting leads to an increase in kinetin concentration, a plant growth regulator [176].

Saprophagous insect farming has recently become a new approach for bioconverting organic wastes into useful products and biofuel [177]. The black soldier fly (BSF) demonstrated a strong capacity to digest the organic material in biowastes [178]. The experiments conducted in this field showed that co-digestate is recommended for BSF farming due to the decrease in heavy metal accumulation [179] and the reduction of pathogens such as *Bacillus* spp., *Salmonella* spp., and *Escherichia coli* [180].

Biochar is a carbon-rich material produced during the pyrolysis process of biomass. The solid fraction of digestate can be used to produce biochar, which is suitable as a solid fuel or soil fertilizer due to its high carbon sink capacity [181]. Biochar obtained from cattle manure and silage co-digestate showed higher performance as a fertilizer than the biochar produced from raw feedstocks. This is a consequence of increased N and P nutrients via co-digestion [182].

The results of the study conducted by Isikhuemhen et al. [183] present the enhancement of mushroom (*Pleurotus ostreatus*) yield when it was cultivated on millet and wheat straw supplemented with solid fraction co-digestate. In contrast, due to its high salt concentration, mono-digestate obtained from feedstocks (like FW) reduced mushroom yield and mycelium colonization [184].

The solid fraction of digestate can also be used as bio-fertilizers after a drying or pelletizing process. In addition, it can be used as solid fuel after a pelletizing process. Furthermore, other methods for the digestate solid fraction valorization are represented by: biofuel production in domestic furnaces, methane recovery via different post-treatments, or production of bioethanol after a mechanical fractionation [185].

6. Perspective Trends

The digestibility of various feedstocks for waste management, bioenergy, and other high-value product generation could be greatly enhanced by co-digestion. AcoD still involves vulnerabilities, though, due to the year-round accessibility of feedstocks, the complexity of feedstocks due to varying rates of biodegradation, and co-digestate safety concerns for agricultural applications, particularly when feedstocks such as wastewater and animal manure are used [38].

If the challenges of AcoD are considered, aspects such as the following can be included:

- Incompatible feedstocks: due to variations in pH levels, nutritional composition, particle sizes, and the anaerobic digestion process may be less effective with some forms of organic waste.
- Process control and monitoring: temperature, pH, and nutrient levels need to be carefully controlled during AcoD to generate the perfect conditions for microbial activity.
- Handling and pretreatment of feedstocks: some feedstocks, such as FW or agricultural residue, may require additional handling or pretreatment before they can be fed to the anaerobic digestion process.
- Potential for process upsets: AcoD technologies might experience process disruptions and reduced productivity because they are susceptible to alterations in the environment and the feedstock's nature.
- Odor and air emissions: anaerobic digestion can produce odors and air pollutants, which need to be regulated to meet standards and have as little of an influence on nearby areas as possible.
- Expensive operating, maintenance, and building costs.

Boosting co-digestive effectiveness is a matter of research among all scientists, disregarding the type of substrate used for the analysis. Difficulties in removing organic matter or other constraints for applying co-digestion are still issues that are met while testing/experimenting. For example, regarding the advancement of lignocellulosic pretreatment using co-digestion, it must be said that there have been several achievements using separated hydrolysis and fermentation (SHF) and simultaneous saccharification and fermentation (SSF), thus obtaining high results in large-scale production. Even though results are positive, the high costs involved in the pretreatment process and the significant metabolic demand of a single microorganism still limit the area of development [186]. Research related to municipal organic solid waste (MOSW) revealed that the majority of research to date has used lab trials to examine the idea of co-digesting MOSW with conductive materials. The complexity of the co-substrate, the quality of the MOSW, the control of iron and carbon-based components, the improvement of the process parameters, and the unfavorable interaction of some other inorganic compounds are still some of the significant challenges with this technology, though. Since it relies on a number of variables, including the variety of substrates, concentration, quantity of metals, and biodegradability, determining the ideal ratio for different substrates can be challenging [187]. Thus, to find the best mixes, it is necessary to research the physicochemical characteristics of the various feedstocks.

In relation to the challenges and perspectives of using AcoD for SS, it must be said that although scientists have intensively studied it for more than 20 years, there are still some limitations that have not been overcome yet. Researchers are still trying to give a definition of high-solid waste and recommend future analyses of the total solids in SS. Furthermore, according to scientific literature, gaining knowledge about the pollutants and their transformation will aid the co-digestion process, making it more efficient by balancing [188].

Despite the study reports that are already available on FOG deposit development in wastewater collection systems and the potential financial advantages of FOG recycling, there are still numerous problems to be solved and theories to be tested. Numerous studies have demonstrated the viability of using yellow grease as a biodiesel feedstock, both from an economic and environmental standpoint [189].

Notwithstanding the social and economic reasons, the effectiveness of lab-scale and industrial-scale biogas systems varied dramatically. These differences are frequently caused by the unpredictability of the waste feedstocks and local environmental aspects in the regions where AD biogas is produced. Due to the uneven distribution of the substrate, it is difficult to use co-digestion to produce the optimum volume of biogas in a certain plant.

Examining the response of a group of microorganisms to the addition of different substances can help create a microbial community that improves the recycling and handling of waste by altering the structure of those substances. To fully understand this process, further research using advanced sequencing techniques is needed to identify and study any unknown microorganisms. Such research will also aid in the optimization, regulation, and simulation of bioreactors by connecting the characteristics of microbial populations to co-digestion models.

7. Conclusions

Numerous studies have demonstrated that AcoD improves the C/N ratio and nutrient balance, increases the methane yield and process stability, and diminishes the concentration of toxic inhibitors through co-substrate dilution.

The main types of substrates used in co-digestion are FW, SS, animal manure, lignocellulosic biomass, algae, FOG, waste from the leather industry, the pulp and paper industry, and others.

The co-digestion process can be improved by applying mechanical, physical, chemical, and biological pretreatments to barely degradable substrates, ensuring an optimal environment for the development of microorganisms.

One of the main advantages of co-digestion is the production of safe and superior-quality co-digestate for agricultural use. Additionally, the co-digestate presents a higher bioavailability of nutrients when it is utilized for composting, vermicomposting, mushroom farming, and black soldier fly growth.

Considering the wide variety of substrates used, co-digestion parameters and conditions, as well as the types of reactors, it is necessary to continue research to clarify as many aspects of the biogas production process as possible.

Advanced techniques in the fields of genomics, proteomics, and metabolomics should be widely utilized to identify and study all the microorganisms present in the digester. Multiple studies will also aid in the optimization, regulation, and simulation of bioreactors by connecting the characteristics of microbial populations to co-digestion conditions.

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