Microbial Degradation in the Biogas Production of Value-Added Compounds

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Abstract

In recent years, there has been an increase in studies aimed at the valorization and recycling of materials, such as by-products, wastewater, and residues from industries and agriculture to produce value-added products such as biogas and biofertilizers. Anaerobic digestion (AD) is considered the main biological route to obtain value-added compounds. AD technology allows the action of microorganisms in four steps whose syntrophic activity of microbial communities transform substrates into biogas without needing to add chemicals, involving low investment, and operating costs. Moreover, there is a variety of substrates that can be used to generate high-value products from AD. In order to better conduct the AD process, several anaerobic digestion technologies have been proposed over the years varying from conventional systems to high-rate reactors and recently co-digestion and soli-state processes. However, understanding and knowing the role of microbial populations involved in AD have become extremely important to promote a better control of anaerobic systems. In addition, it ensures nutritional

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and operational conditions to favor the biochemical route for the biomethane generation. Therefore, research opportunities regarding the syntrophic metabolism that occurs throughout each step of the microbial degradation is essential for anaerobic decomposition of many substrates and the stability of biogas production. This type of scientific study can help to improve the sustainability and energy balance from using material that is being discarded in the environment.

Keywords

Anaerobic digestion · Add-value bioproducts · Syntrophic activity · Microbial population · Biogas production

3.1 Introduction

The global energy matrix is based on using nonrenewable sources such as oil, coal, and natural gas (Pareek et al. 2020). In contrast, these sources applied in conventional energy production processes, such as chemical and thermochemical processes, generate pollutants that contribute to greenhouse gas emissions and consequently unfavorable impacts including global warming and climate change (Ahmed et al. 2019; Hill 2009). Thus, an increase can be observed in studies focusing on the valorization and recycling of materials, such as by-products, wastewater and residues from industries and agriculture to produce value-added products, such as biogas. This is because this type of material known as biomass contains high amounts of proteins, sugars, and lipids that can be considered as cheap and abundant raw materials for the synthesis of value-added chemicals and biomaterials (Ahmed et al. 2019; Murthy and Madhava Naidu 2012).

The main biological process used to obtain value-added compounds is anaerobic digestion (AD). AD is considered a green route to produce bioenergy, especially due to the action of microorganisms without needing to add chemicals, involving low investment and operating costs (Cesaro and Belgiorno 2014). AD has been used for many years, and it comprises a natural four-step process including hydrolyses, acidogenesis, acetogenesis, and methanogenesis in which different microbial groups are syntrophically associated with the conversion of organic compounds primarily into biogas, which has methane as a relevant component (Grangeiro et al. 2019). Moreover, during AD, nutrient-rich solid and liquid residues, also known as digestate, are produced and can be applied as a biofertilizer for soil conditioners (Apergis et al. 2016; Kirk-Davidoff 2018). Therefore, AD is considered a process that involves a broad range of value-added bioproducts which can be obtained from a single type of raw material (Grangeiro et al. 2019). As show in Fig. 3.1, a large range of microorganisms are involved in all four steps of AD of carbohydrates, lipids, and protein.

Several studies worldwide have demonstrated the use of different feedstocks as waste as well as wastewater from industrial and agro-industrial processes to produce biogas. Regarding industrial feedstock, there are many studies such as those on

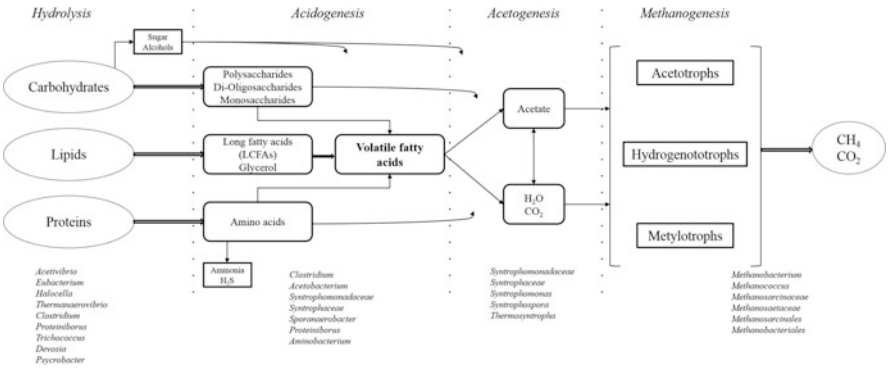


Fig. 3.1 Metabolic sequences and principal microbial family groups involved in the anaerobic AD of carbohydrates, lipids, and protein. Source: Adapted from Campanaro et al. (2016)

cheese whey (Azbar et al. 2009; Damasceno et al. 2008), cassava wastewater (Jiraprasertwong et al. 2019; Olukanni and Olatunji 2018), whey (Erguder et al. 2001; Luo and Angelidaki 2013), dairy and food processing wastewater (Ahmad et al. 2019; Tikariha and Sahu 2014), breweries (De Araujo et al. 2016), wineries (Basset et al. 2016), soft drinks (Kalyuzhnyi et al. 1997), and others. Some studies reported using glycerin-based wastewater (Amon et al. 2006; Astals et al. 2011) and sulfate-rich wastewater (Sarti et al. 2011). Moreover, different agricultural crops and terrestrial and aquatic plants are used as feedstock for AD (Gunaseelan 1997).

Although biogas production from anaerobic systems is considered a well-established technology for different feedstocks, it is very important to understand the role of microbial populations during the process considering the influence of operational parameters in these systems. Because of that, several studies have proposed innovations for AD performance, including biological strategies and innovating control systems (Tabatabaei et al. 2020).

This chapter provides information about microbial degradation in biogas production from biomass through AD. In the first part, common substrates used to generate products with added value from AD are described. The second part discusses the AD stages and the specific microbial population required in each stage. Afterward, the key factors that influence the microbial community structure during the anaerobic process are investigated. Finally, these anaerobic digestion technologies proposed over the years, as well as new system approaches to enhance biogas production using microbial degradation, are discussed. To sum up, this chapter compiles essential information to better understand the potential of AD as a simple and robust bioprocess for recovery bioenergy.

3.2 Substrates Commonly Used in Biogas Production

The substrates used during microbial degradation to generate biogas are primarily organic matter considered as waste, thus resulting in a wide range of raw materials. The composition and physical–chemical structure of the substrate can directly affect the microbiological complex system that favors anaerobiosis, which can greatly affect the stability and biodegradation efficiency of the process (Sharma et al. 1988).

Therefore, substrate characterization is important to ensure microbial nutritional needs, operational conditions, and, consequently, to predict the amount and quality of biogas that can be produced. These factors are intricately linked to the available nutrients and recalcitrant compound content in the substrate. Furthermore, the fractionation of the substrate will depend on the size of its particles, which can benefit or hinder the hydrolysis phase (Aziz et al. 2020; Sharma et al. 1988). Thus, the choice of the process, according to the available raw material, influences the results, which can maximize the production of bioenergy and its quality.

During the anaerobic digestion process, the presence of macro- and micronutrients, as well as trace elements, is necessary for microbial community growth and stability. Carbon, nitrogen, phosphorus, and sulfur must be present in a ratio of about 600:15:5:1 (Sharma et al. 1988; Mata-Alvarez et al. 2014). The carbon–nitrogen (C:N) ratio is the most important process indicator whose ideal range is reported to be ranging from 20 to 35; for instance, substrates rich in proteins can generate high levels of ammonia leading to ammonia accumulation in the medium and can thus irreversibly impair the AD progress (Puñal et al. 2000). The trace elements are especially important when the process is mono-digestion, i.e., only one type of substrate is used during AD. In this case, iron, cobalt, selenium, nickel, molybdenum, and tungsten must be added to the process in case the substrate does not have sufficient amounts for maintaining the microorganisms (Aziz et al. 2020; Bohutskyi and Bouwer 2013; Schattauer et al. 2011).

In fact, biogas and biofertilizer production was not the primary focus of AD processes. This technology was used only to reduce aerobic sludge excess from sewage treatment plants and in the treatment of animal manure, but the biogas generated was not reused for energy purposes. Hence the use of this technology was mainly associated with these two activities, which were the main sources of substrate, currently, for biogas generation (Milanez et al. 2018). However, after the oil crisis in 1980, several studies investigated using different types of biomass with the primary aim of producing good yield and quality of biogas (higher methane content) along with low implementation and operational costs. Currently, agricultural waste, municipal sewage, organic industrial waste, food waste, solid organic municipal waste, aquatic biomass, forest waste, and energy crops have been used in AD processes (Divya et al. 2015; Martínez-Gutiérrez 2018; Pérez-Chávez et al. 2019; Shrestha et al. 2017).

Within this context, choosing the most suitable substrate for biogas production depends on the purpose of the generating unit. If the biogas generated is in plants with main activities in other segments, the substrate will already be defined and the type of application of AD should be chosen according to the characteristics of the

Table 3.1 Biogas yield and potential to generate biomethane from the most common feedstock used in the AD process

Feedstock	Biogas yield	Potential to generate biomethane (bcm)[a]
Livestock manure	40–80 m^3/ton DW[b]	250 to 370
Sewage	18–26 L/person-day	22 to 32
Food waste	150–180 m^3/ton FW[c]	85 to 100
Crop residues	~10 m^3/m^3day	300 to 380
Energy crops	3500–9000 m^3/CH_4 hectare	330 to 490

Source: Adapted from Milanez et al. (2018) and Jain (2019)
[a]Billion cubic meters
[b]Dry weight
[c]Fresh weight

substrate generated in that plant. Otherwise, if the intention is a biogas plant, the political and geographical context must be considered, as the type of substrate available in the region for plant feeding, logistics, and tax incentives must be analyzed. For example, in Germany, a country recognized as a world leader in the production of energy from biogas, there is a strong government incentive to generate energy from renewable sources, mainly due to the governmental project to deactivate nuclear power plants. The Könnern plant, in Germany, is one of the largest biogas parks in the world, and the main substrates are derived from agriculture, such as animal waste, agricultural residues, and energy crops (Purkus et al. 2017).

Based on prior knowledge about the type of substrate available for biogas generation, the maximum biogas production can be estimated by the Biogas Generation Chemical Potential, in which the amounts of carbohydrates, proteins, fats, and other compounds refer to the chemical equation involved in the bio-digestion of specific substrates. (Mélo-Schlub et al. 2019; Penteado et al. 2017). In addition to determining the technology to be used, it is possible to accurately calculate the maximum amount of biogas that will be produced. Therefore, it is essential to know the composition of the substrate to be used for biogas production because from this choice the best technological model can be planned for the effective construction of the plant, considering that the size of the bioreactor or digester will depend on the type of substrate and its potential for biogas generation (Li et al. 2017; Weiland 2010).

Table 3.1 shows the participation of the different types of substrates most used in the world for biogas generation and the energy potential of each, if all this material, which is mostly waste, were fully recovered for the bioenergy generation (Jain and Jain 2019; Milanez et al. 2018).

The composition of plant derivatives comprises different polysaccharides. These polysaccharides are formed by carbohydrates linked in straight or branched chains; the structure will vary according to the composition of each biomass. Lignocellulosic biomass, in which the plant cell wall has a predominant presence of cellulose, hemicellulose, and lignin, as plants, are considered of greater complexity for microbial degradation, mainly due to the presence of lignin. The higher the concentration of lignin in the biomass structure, the more difficult and time consuming it will be to

degrade and generate biogas; for instance, forest waste, which has a rigid structure in its largest portion. Cellulose and hemicellulose are relatively easily degradable as well as the simplest polysaccharides (starch and glycogen, pectin, etc.) (Azman et al. 2015; Lynd et al. 2002; Sánchez and Cardona 2008).

The greatest advantage of using plant biomass is related to its abundance and energy potential, which can boost biogas production worldwide. However, the composition of plant biomass can hinder the action of microorganisms; therefore, according to the nature of the biomass, pretreatments as well as long periods of hydraulic retention for digestion are necessary to enable the AD process (Sánchez and Cardona 2008; Wagner et al. 2018). Thus, several studies have been carried out to improve the efficiency of AD involving lignocellulosic materials, for instance the co-digestion of various residues, such as biomass fractionation investigations.

To reuse lignocellulosic biomass in its entirety, many alternatives to improve biogas production have been reported in the literature, such as the use of microalgae, biomass from phytoremediation, residues from insect production, and the substrate of the cultivation of edible fungi (Bulak et al. 2020; Klassen et al. 2016; Kumar et al. 2020; Łochyńska and Frankowski 2018; Ma et al. 2015; Zabed et al. 2020). In addition, to improve the process, co-digestion with commonly used substrates, such as food residues, agricultural residues, and urban pruning residues, among others have been used (Bedoić et al. 2020; Chowdhury et al. 2020; Issah et al. 2020; Parsaee et al. 2019; Vassalle et al. 2020; Wang et al. 2018).

Most substrates of this nature have proteins, which are long chains formed by amino acids form peptide bonds or amides. Several amino acids are considered essential for the cellular maintenance of living beings, and there are more than 20 different types, which when combined can form molecules from simple to complex. These structural characteristics can influence their solubility, as well as influence the release of smaller molecules, which would hinder the microbial degradation of these compounds (Angelidaki et al. 2011). Protein-rich substrates are already used in biogas production, usually from livestock residues, such as animal manure, slaughterhouse waste, and dairy products; in the production of ethanol, residues generated during the distillation stage, such as vinasse, and food industry wastewater (Banks et al. 2012; Luo et al. 2016; Rajagopal et al. 2013; Solli et al. 2014).

The lipid residues, with high levels of fats, are complex molecules of different sizes that can be saturated or unsaturated, and when this type of molecule breaks down, long-chain fatty acids (over 12 carbons in their structure) are generated as well as glycerol (Dasa et al. 2016). The main sources of lipid-rich substrates for biogas production are activities directly linked to the generation of excess fats, such as domestic sewage and industrial effluents, specifically from slaughterhouses, dairy products, wool washing water, processing vegetable oil for human consumption, and grease retention sludges (Affes et al. 2017; Bong et al. 2018; Luostarinen et al. 2009; Sousa et al. 2009; Souza et al. 2009; Xu et al. 2018a). In addition, current studies have demonstrated that algae and microalgae also have lipid-rich composition (Ma et al. 2015). Lipid substrates are commonly considered an excellent source of raw material for biogas generation (Table 3.2), which can produce higher amounts of

Table 3.2 Biogas production and methane content of feedstocks rich in carbohydrates, proteins, and lipids, respectively

Component	Biogas (L/g)	CH_4 (%)
Carbohydrates	0.830	50.0
Proteins	0.921	69.8
Lipids	1.425	69.5

Source: Adapted from Alves et al. (2009) and Wang et al. (2018)

methane than sources rich in carbohydrates and proteins (Leung and Wang 2016; Li et al. 2017).

Despite the diversity of substrates that can be used to produce biogas rich in methane, attention is needed with the microbiota involved in the system. Protein-rich substrates tend to release high levels of ammonia, which inhibits methanogenic archaea. Substrates rich in carbohydrates can negatively affect AD due to their rapid degradation when compared to protein and lipid materials, leading to an imbalance of the C:N ratio. Consequently, carbohydrate-rich feedstocks can limit the availability of nutrients and cause acidification of the fermentative medium, mainly due to the accumulation of organic acids, which can enhance hydrogen production (De Gioannis et al. 2013; Li et al. 2017; Meng et al. 2015; Paritosh et al. 2017; Xu et al. 2018a).

Some studies have pointed out that substances rich in lipids have a better chemical potential for generating biogas than carbohydrates and proteins, although these are more easily degradable during the AD process. However, during the hydrolysis stage, the release of long-chain fatty acids can lead to inhibition of methanogen, due to the destruction of the cell membrane of microorganisms. Therefore, the hydrolysis of lipids can be the limiting step for AD of substrates rich with this compound (Cirne et al. 2007; Cuetos et al. 2008; Leung and Wang 2016; Sun et al. 2014; Yuan and Zhu 2016; Zhang et al. 2014).

Notably, the individual influence caused by specific compounds in the AD process can be extremely disadvantageous due to its composition. Thus, several studies have been developed to demystify the role of organic composition in the efficiency of AD from mono-digestion and its impacts on the microbiota (Alibardi and Cossu 2016; Li et al. 2016; Rajagopal 2013; Wang et al. 2014; Yin et al. 2014) as in co-digestion, associating substrates rich in different compounds to be complementary (Astals et al. 2011; Koch et al. 2015; Zhang et al. 2013).

It is worth mentioning that regarding substrates from domestic sanitary sewage and food waste, the organic composition varies greatly concerning geographic and cultural location, which are influenced by consumption patterns, food preparation, and seasonal changes (Kobayashi et al. 2009; Meng et al. 2015; Xu et al. 2018b).

3.3 Anaerobic Digestion Pathways and Diversity of Microorganisms Involved

As previously presented, there is a variety of substrates that can be used to generate high-value products from AD (biogas and biofertilizers). However, substrates with high-energy potential (organic composition) can also cause stress in the operating system, resulting in a less stable process (Cuetos et al. 2008). When the system is out of balance, the digestion of organic material can become suboptimal, making insufficient use of it leading to a decline in the production and quality of biogas.

In order to better conduct the AD process so that the generation of value-added products can be optimized, the understanding of the syntrophic activity of microbial communities involved in the AD has become extremely important. Moreover, microbial functions as well as the impacts promoted by the different aspects that may occur during bio-digestion have gained notoriety as an essential factor to ensure the efficiency and stability of the process. By knowing and understanding the present microbiota, nutritional and operational conditions can be ensured to favor the biochemical route for biomethane generation (Vanwonterghem et al. 2014).

AD is a biochemical process divided into several stages, and a specific microbial population is required in each stage. Harper and Pohland (1987) reported that there are at least nine different biochemical mechanisms involved in the microbial degradation of organic materials during AD. However, four main stages are considered: hydrolysis, acidogenesis, acetogenesis, and methanogenesis. As the microorganisms are the nuclei of the digesters, researchers have endeavored to identify, within the microbial groups, the main microorganisms responsible for producing methane and their functions according to the stages and operational conditions.

3.3.1 Hydrolysis/Acidogenesis

The first phase is coordinated by hydrolytic and acidogenic bacteria and probably fungi. This group of microorganisms is responsible for the conversion of complex organic compounds (hydrolysis)—such as polysaccharides, lipids, proteins—and simpler organic compounds (acidogenesis)—such as long chain fatty acids (LCFA), glycerol, sugars, amino acids, etc.—in volatile fatty acids (acetate, propionate, butyrate, lactate, valerate, caproate, etc.), alcohols, formiate, hydrogen, and carbon dioxide, which further will be used in the following steps (Kandylis et al. 2016).

The degradation of these compounds occurs from extracellular enzymes secreted by bacteria in the fermentation medium or may be present in the cell wall (Azman et al. 2015; Kazda et al. 2014; Schnürer 2016). It is known that in the stages of hydrolysis and acidogenesis there are about 50 bacterial species known and described in different AD processes (Balk et al. 2002; Seon et al. 2014; Yamada et al. 2006).

Normally, hydrolysis of materials rich in carbohydrates is one of the simplest metabolic pathways of AD; it is easily degraded to glucose, which facilitates the

following steps. In lignocellulosic substrates, cellulose is hydrolyzed to glucose, and cellobiose and hemicelluloses are converted into monomers and acetic acid. In this case, the bacteria have an enzymatic complex in their cell wall (celluloses), which has proteins that identify and bind to the cellulose, making the degradation the more efficient. However, the fungi act differently, by adhering to the cellulose surface and penetrating plant cell walls of complex biomass (Ding et al. 2012; Kazda et al. 2014; Schnürer 2016). Hydrolytic microorganisms acting in AD have been investigated to optimize the use of plant biomass entirely from pretreatments which increase substrate readily available (Chowdhury et al. 2020; Issah et al. 2020; Li et al. 2019; Tabatabaei et al. 2020).

Bacteria affiliated to phylum Firmicutes, Bacteroidetes, Fibrobacteres, Spirochaetes, Proteobacteria, Cloacimonetes, Actinomyces, and Thermotogae are the most common microorganisms responsible for degradation of complex molecules into simpler compounds. The most common genera reported are *Acetivibrio, Butyrivibrio, Caldanaerobacter, Caldicellulosiruptor, Clostridium, Eubacteruim, Halocella, Ruminoclostridium, Ruminococcs, Bacteroides, Paludivacter, Fibrobacter, Espiroquetas, Treponema, Fervidobacteria, and Thermotoga* (Azman et al. 2015; Campanaro et al. 2016; Chen et al. 2016; Jia et al. 2018; Lebuhn et al. 2014; Liu et al. 2017, 2018; Seon et al. 2014; Sun et al. 2016). The anaerobic fungi present in hydrolysis are associated with the phylum Neocallimastigomycota. In fact, fungi of this nature are generally found in the digestive system of ruminants, playing an important role in the degradation of lignocellulosic material (Cheng et al. 2018; Dollhofer et al. 2015).

Proteins are hydrolyzed to amino acids by the action of extracellular enzymes, known as proteases. Amino acids can be degraded by the Stickland reaction (a donor amino acid and another electron receptor), which promotes oxidation, producing volatile carboxylic acids that are smaller than the original amino acid (Fig. 3.2a). Alanine, for example, has a three-carbon chain and during this reaction, it is converted to acetate (Ramsay and Pullammanappallil 2001). For example, means containing gelatin are converted to methane through the Stickland reaction, in which alanine (donor) and glycine (recipient), gelatin components, are converted to acetate as shown in Fig. 3.2b (Ramsay and Pullammanappallil 2001; Sangavai et al. 2019).

Amino acids can also suffer from oxidized action (released hydrogens). This route only occurs in symbiosis with hydrogen receptors, such as hydrogenotrophic methanogens, which keep the partial pressure of hydrogen low in the fermentation medium. Despite having two hydrolytic pathways for amino acids, the result of this degradation will always release the amino group in the form of ammonia, and the sulfur from cysteine and methionine is released as hydrogen sulfide (Fig. 3.3) (Schink and Stams 2013).

The main microorganisms involved in the degradation of materials rich in proteins and amino acids are from the phylum Firmicutes, and the most common genera reported are *Anaeromusa, Anaerosphaera, Aminobacterium, Aminomonas, Gelria, Peptoniphilus, Thermanaerovibrio* (Baena et al. 1999, 2000; Plugge et al. 2002; Tomazetto et al. 2014; Ueki et al. 2009), *Clostridium* (Tang et al. 2005), *Proteiniborus* (Hahnke et al. 2018) and *Sporanaerobacter* (Hernandez-Eugenio

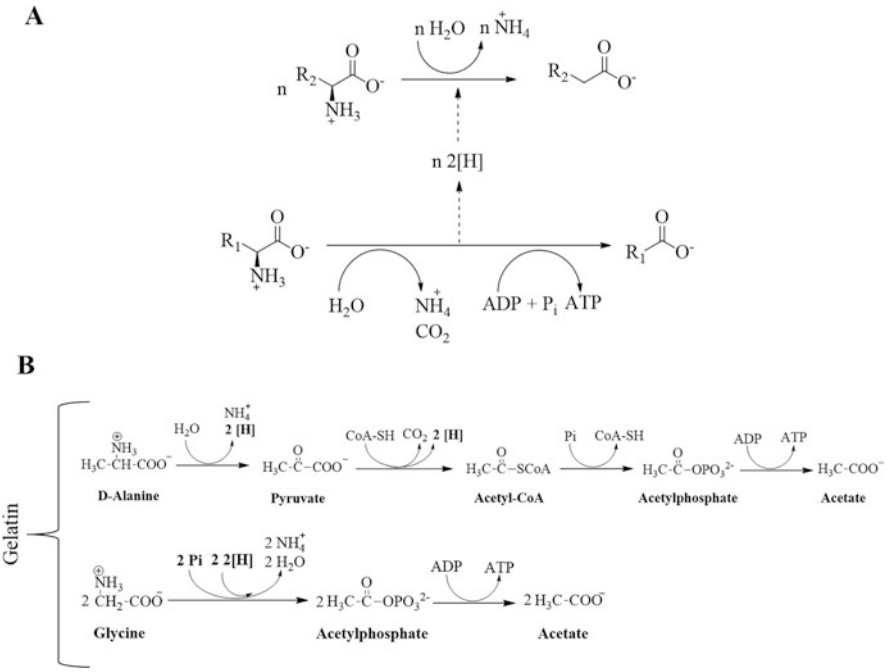


Fig. 3.2 General Stickland reaction (**a**) Stickland reaction on Alanine and Glycine (**b**). Source: Adapted from Ramsay and Pullammanappallil (2001) and Sangavai et al. (2019)

$$C_3H_6O_2NS\ (Cys) + 2H_2O \longrightarrow C_2H_4O_2\ (acetate) + NH_3 + CO_2 + H_2S + 1/2H_2 + ATP$$

$$C_5H_{11}O_2NS\ (Met) + 2H_2O \longrightarrow C_3H_6O_2\ (propionate) + CO_2 + NH_3 + CH_4S + H_2 + ATP$$

Fig. 3.3 Cysteine and methionine degradation reactions in the methanogenic pathway

et al. 2002). However, other studies have indicated that bacteria from the phyla Bacteroides, Fusobacteria, and Cloacimonetes can have acidogenic metabolic activity for amino acids during AD (Hahnke et al. 2016; Stolze et al. 2018).

The degradation of lipid material occurs by extracellular lipases, which catalyze the hydrolysis reaction at the water–lipid interface. After the action of lipolytic bacteria, LCFAs and glycerol are released (Mendes et al. 2012; Stergiou et al. 2013). There is still little knowledge regarding bacteria that degrade lipids in AD. For instance, lipolytic bacteria in AD, such as microorganisms from the phylum Firmicutes, Bacteroidetes, Spirochaetes, and Proteobacteria, have been proposed. Bacteria of the family Caldilineaceae, Bacteroidaceae, and the genera *Trichococcus, Devosia,* and *Psycrobacter* are reported to be the main agents involved in the degradation of fat-rich material (Li et al. 2013; Nakasaki et al. 2020; Petropoulos et al. 2018).

Moreover, the hydrolysis stage requires microorganisms with specific characteristics, according to the substrate. As the first phase of AD, these

microorganisms end up being the most energetically benefited (de Aquino and Chernicharo 2005). After this stage and the release of simpler compounds, the microorganisms found in the subsequent stages can be considered predominant in specific phyla, such as the phylum Firmicutes, in which bacteria from this group are present in the hydrolytic and fermentative stages during AD as well as in different reactors and substrates (Sanz et al. 2017; Wang et al. 2018).

3.3.2 Acetogenesis/Methanogenesis

Acetogenic bacteria are microorganisms that convert intermediate organic compounds generated in the acidogenesis and hydrolysis stages. These bacteria have the highest growth rate (~30 min) of the anaerobic community for biogas generation due to the abundance of hydrolysate released, which is directly influenced by the hydrolysis of organic material (de Aquino and Chernicharo 2005; Kandylis et al. 2016). Acetogens convert the hydrolyzed material into acetate, hydrogen, and carbon dioxide as the main products and can use nitrate, sulfate, and even CO_2 as electron receptors during the reaction (Ragsdale and Pierce 2008). They can also use hydrolysis products directly to produce acetates, such as carbohydrates and amino acids, and can oxidize pyruvate to acetate, which is a very common by-product generated during AD (Drake et al. 2008; Schink and Stams 2013).

Most reactions carried out by acetogenic bacteria only occur if the partial pressure of hydrogen is low, such as the oxidation reactions of organic acids of short and long chains (Schink 1997). This happens due to thermodynamic reasons, and when the whole microbiological context of AD is analyzed, the energetic condition of the acetogens is less favorable regarding the methanogenic archaea; however, there is a symbiosis between these microorganisms, known as syntropy. The interaction between both groups promotes enough energy for their growth, and therefore acetogens need methanogens and vice versa (Drake et al. 2008; Schink 1997; Schink and Stams 2013). However, there may be an imbalance between these communities causing competition for the substrate and malfunction of the system. The main intermediate products generated in the previous steps and their respective chemical reactions for acetate generation are shown in Table 3.3.

In this case, the main methanogenic pathways (aceticlastic and hydrogenotrophic) are affected by the unbalanced presence of homoacetogens and acetate oxidative bacteria, according to the concentration of acetate and H_2 (main methanation substrates), and thermodynamically unfavorable competition may occur. For example, hydrogenotrophic homoacetogens and methanogens (MH) compete for H_2 to convert CO_2 into acetate and methane, respectively, according to the general equations presented in Table 3.4. Ideally, homoacetogens coexist with aceticlastic methanogens, maintaining sufficient acetate and H_2 concentrations for their maintenance (Lee et al. 2015). Table 3.4 shows some homoacetogenic and hydrogenotrophic microorganisms and their respective H_2 demands.

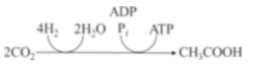
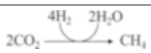
Acetogenic bacteria are generally attributed to the genera *Clostridium* and *Acetobacterium* (phylum Firmicutes), but bacteria from the phylum Proteobacteria

Table 3.3 Acetogenic decomposition of intermediate products

Intermediate products	Chemical reaction to acetate
Propionic acid	$CH_3(CH_2)COOH + 2H_2O \rightarrow CH_3COOH + CO_2 + 3H_2$
Butyric acid	$CH_3(CH_2)_2COOH + 2H_2O \rightarrow 2CH_3COOH + 2H_2$
Valeric acid	$CH_3(CH_2)_3COOH + 2H_2O \rightarrow CH_3COOH + CH_3CH_2COOH + 2H_2$
Isovaleric acid	$(CH_3)_2CHCH_2COOH + HCO_2H + 2H_2O \rightarrow 3CH_3COOH + 2H_2$
Caproic acid	$CH_3(CH_2)_4COOH + 4H_2O \rightarrow 3CH_3COOH + 5H_2$
Glycerin	$C_3H_8O_3 + H_2O \rightarrow CH_3COOH + CO_2 + 3H_2$
Lactic acid	$C_3CHOHCOOH + 2H_2O \rightarrow CH_3COOH + HCO_3 + H^+ + 2H_2$
Ethanol	$CH_3(CH_2)OH + H_2O \rightarrow CH_3COOH + 2H_2$

Source: Adapted from Chernicharo (2007) and Deublein and Steinhauser (2010)

Table 3.4 Example of homoacetogens and hydrogenotrophs, chemical reactions and demand for H_2

	Reactions	Species	H_2 (ppm)
Homoacetogens		*Sporomusa termitida*	830
		Acetobaeterium woodii	520
		Aeetobacterium carbinolicum	950
Hydrogenotrophic		*Methanospirillum hungatei*	30
		Methanobrevibacter smithii	100
		Methanobrevibacter arboriphilus	90
		Methanobaeterium formicum	28
		Methanococeus vannielii	75

Source: Adapted from Cord-Ruwisch et al. (1988)

were also mentioned with metabolic activity in these stages (Azman et al. 2015; St-Pierre and Wright 2014).

Regardless of the lipid degradation, glycerol is released after hydrolysis, which is easily converted into volatile fatty acids (VFA). LCFAs demand specific groups of microorganisms to convert them into VFA, as they need to be transported across the cell membrane of acetogenic bacteria, where they are converted to acetate, CO_2, and H_2 via the β-oxidation pathway (Ma et al. 2015; Nakasaki et al. 2020; Weng and Jeris 1976). The bacteria from the Syntrophomonadaceae and Syntrophaceae families have been identified (Sousa et al. 2009; Ziels et al. 2018), associated with phylum Firmicutes and Proteobacteria, respectively, within the ability to degrade long-chain acids in syntropy with methanogenic archaea.

The degradation of short-chain fatty acids (acetate, propionate, butyrate, etc.) in syntropy with methanogens are well distributed in the phylogenetic scope. The genera *Syntrophomonas, Syntrophospora, Syntrophothermus, Thermosyntropha* and *Pelotomaculum* (phylum Firmicutes), and the genera *Syntrophus, Smithella* and *Syntrophobacter* (phylum Proteobacteria) are described as propionate and butyrate syntrophic bacteria in AD systems (Worm et al. 2014). On the other

hand, microorganisms affiliated to the phylum Cloacimonetes and Chloriflexi are reported to be capable of growing in syntropy with hydrogenotrophic methanogens (Li et al. 2015; Nobu et al. 2015; Pelletier et al. 2008).

The genera *Clostridium, Thermoacetogenium, Syntrophaceticus* and *Tepidanaerobacter*, all from the phylum Firmicutes are the main oxidative bacteria of syntrophic acetate (Westerholm et al. 2016). However, bacteria of the order Clostridiales, Thermoanaerobacterales, Synergistes, the genus *Coprothermobacter*, and the phylum Spirochaetes, Thermotogae, Chloroflexis and Bacteroidetes have been reported as possible oxidants of syntrophic acetate (Bassani et al. 2015; Ho et al. 2014; Ito et al. 2011; Lee et al. 2015; Mosbæk et al. 2016; Müller et al. 2016; Ruiz-Sánchez et al. 2018; Westerholm et al. 2018; Zakrzewski et al. 2012). It was observed that the presence of the genus *Syntrophomonas*, which degrades propionate and butyrate, and the phylum Synergistetes, which are oxidizers of syntrophic acetate, may indicate good acetogenic performance (He et al. 2017; Lienen et al. 2014) and acetotrophic (Schink and Stams 2013), respectively. However, further research is needed to characterize and elucidate the performance of these bacteria during AD.

The last stage of the AD is considered the limiting phase, which comprises methanogenic archaeal. This group of microorganisms is mainly responsible for producing methane and belong to the phylum Euryarchaeota, in which about 65 species are active in the methanogenesis of AD, divided into 4 orders, 8 families and 19 genera (Imachi et al. 2007; Lee et al. 2014; Nielsen et al. 2007; Sousa et al. 2007b; Wang et al. 2018). The methanogenic community normally corresponds to a small portion of the total community (around 2 to 5%) and its growth is considered slow (from 6 hours to 3 days) concerning the other microorganisms involved in AD (Mosey 1983). However, its metabolic activity, with its abundance, is considered high.

The main microorganisms identified in anaerobic reactors are of the order Methanobacteriales, Methanocellales, Methanomicrobiales, Methanosarcinales, Methanococcales, and Methanomassiliicoccales (Enzmann et al. 2018; Lee et al. 2014; Schnürer 2016). The genera *Methanobacterium, Methanococcus, Methanobrevibacter, Methanomicrobium, Methanosarcina, Methanoculleus*, and *Methanosaeta* are considered the main methanogenic arch responsible for the generation of biomethane (Imachi et al. 2007; Nielsen et al. 2007; Sousa et al. 2007b). In thermophilic reactors, the emphasis is given to the genera *Methanoculleus* and *Methanothermobacter* (Carballa et al. 2015; Lee et al. 2014; Sasaki et al. 2011; Ziganshin et al. 2013).

Methanogenic archaeal have three known metabolic pathways for methane release. These routes were divided according to the precursor substrate (Costa and Leigh 2014; Liu and Whitman 2008):

- Aceticlastic route: In this pathway, the acetate is reduced to a methyl group and CO_2. The methyl group is reduced to methane after electron donation from the carboxyl group.

- Hydrogenotrophic route: CO_2 is reduced to CH_4 using H_2 or formiate as electron donors.
- Methylotrophic route: Methylated compounds, such as methanol, methylamines, and methyl sulfides, are used to generate CH_4. In this case, most methylotrophic methanogens use CO_2 as electron donors to oxidize methyl groups.

The main microbial community responsible for biogas production belongs to the group of aceticlastic methanogens since the degradation of organic matter in AD systems depends on the conversion of acetate into methane (VanBriesen 2001). So far, it is known that acetate is used exclusively by microorganisms from the families Methanosarcinaceae and Methanosaetaceae (order Methanosarcinales). Methanosarcinaceae microorganisms stand out due to their ability to grow on different substrates and they can consume hydrogen and methanol, as well as acetate, making them more versatile than the Methanosaetaceae group, which are strictly consumers of acetate (De Vrieze et al. 2012).

Hydrogenotroph microorganisms are present in almost all methanogenic orders, except in the order Methanomassiliicoccales whose metabolic characteristic was not observed (Enzmann et al. 2018). Therefore, this route is not considered as the main route for methane generation due to possible competition with other microorganisms. However, studies have indicated that hydrogenotrophic methanogens are more resistant to stressful conditions than acetoclastic. In this case, when the acetate concentration decreases, the hydrogenotrophic can act in symbiosis with oxidative acetate bacteria and maintain mechanization. This microbial diversity with different metabolic routes makes AD a complex and resilient process (Bialek et al. 2012; Cho et al. 2013; Ma et al. 2013; Madsen et al. 2011; Sousa et al. 2007a; Steinberg and Regan 2011; Werner et al. 2014). Figure 3.4 shows an example of syntrophy between acetogenic bacteria and hydrogenotrophic for the degradation of ethanol to methane.

The *metanosarcina* genus is known to use all known methanogenic metabolic pathways (Fig. 3.5) i.e., the microorganisms of this genus can be hydrogenotrophic, acetoclastic, and methylotrophic. Besides, they are the only known species with this ability and can metabolize at least nine methanogenic substrates (Galagan et al. 2002). However, the production of methane from methylated compounds is also carried out by archaeal of the orders Methanomassiliicoccales, Methanobacteriales and Methanosarcinales (Enzmann et al. 2018), and the WSA2 class was proposed as a methylate reducer restricted to methanogenesis (Nobu et al. 2016).

Notably, the microbial community involved in AD is complex, and the success of the process depends strictly on the syntrophic interactions between them since several environmental factors can intervene in this microbial symbiosis. After identifying the groups and their respective functions, engineering and management techniques can be used, which makes it essential to model development strategies and process optimization (Carballa et al. 2015; Koch et al. 2014). However, these consortia are not fully understood, as most microorganisms are not cultivable at the species level, and metagenome studies indicate a large number of sequences that make it difficult to classify all species present in the system, with taxonomically

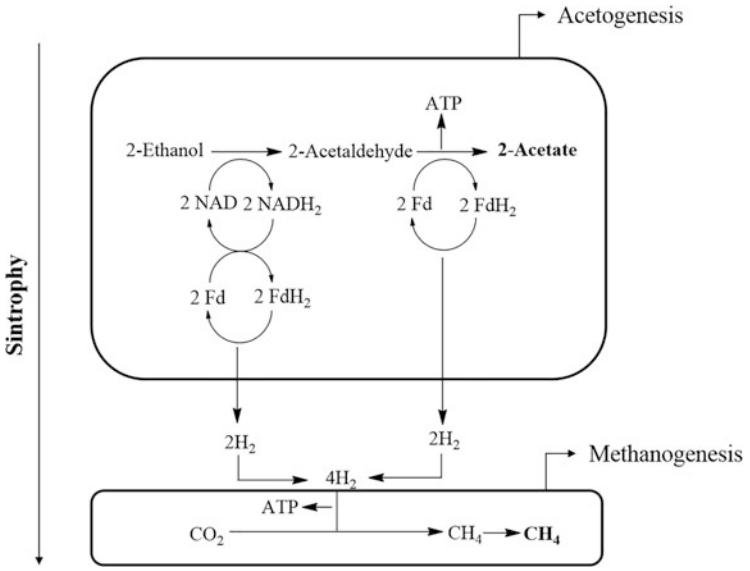


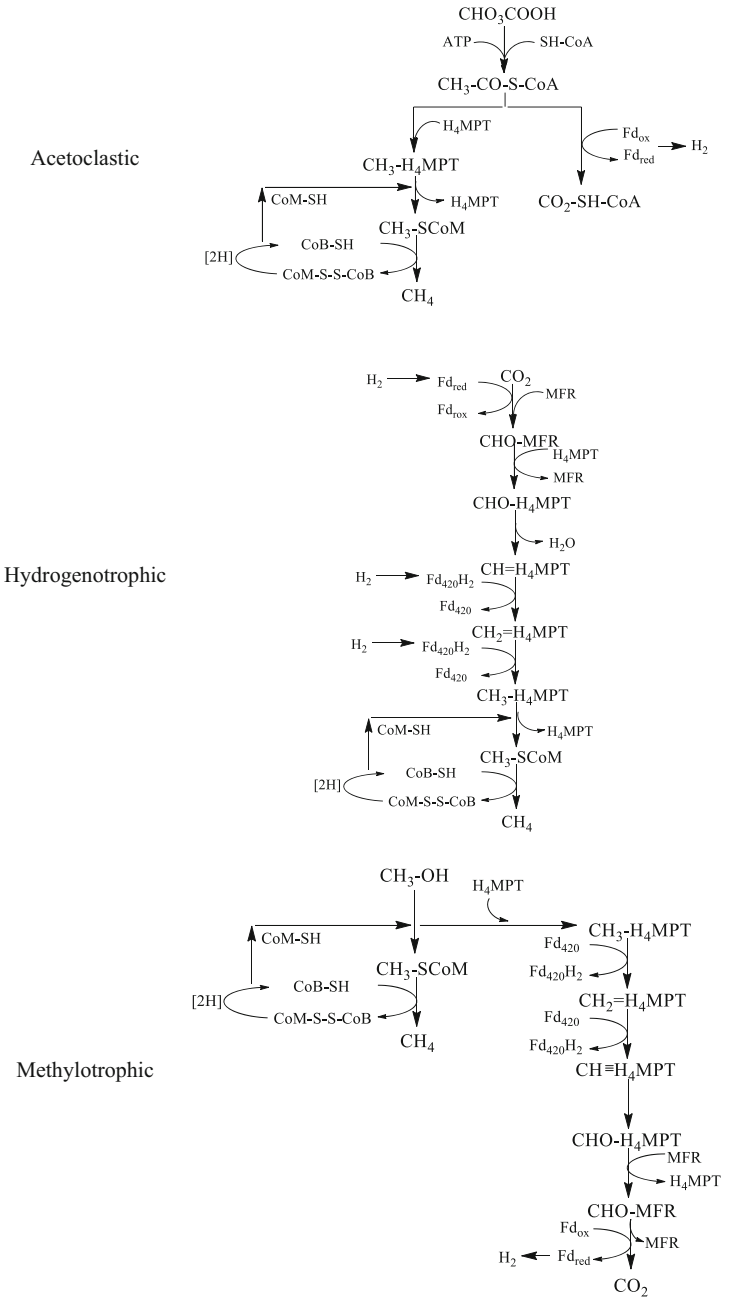
Fig. 3.4 Syntrophy between acetogenic bacteria and hydrogenotrophic. Source: Adapted from Deublein and Steinhauser (2010)

reported levels higher (such as phylum, order, family, and genus). Therefore, most microbial species are unknown in AD (Campanaro et al. 2016).

Molecular biology techniques, such as PCR and its derivatives, in conjunction with genomic sequencing technologies (16S rRNA) have brought continuous advances for the identification, at the species level, of the microbiota involved in AD. As the analytical techniques become more sophisticated, future studies can be carried out and the list of anaerobic microorganisms will tend to increase. Identification studies of species involved in AD can also elucidate the degradation of different chemical compounds frequently made by members of the same genus, which would enable a better understanding of the metabolic biochemical routes and the syntropy in the anaerobic community for biogas generation. Omics approaches in conjunction with new species isolation technologies can significantly contribute to a better understanding of functions at the cellular level (De Vrieze et al. 2018; Hassa et al. 2018; Maus et al. 2018; Stolze et al. 2016).

3.4 Key Factors Imposed on Microorganisms that Affect Biogas Productivity

Stability of biogas production is greatly dependent on the microbial community stability of anaerobic reactors. Temperature, pH and the organic loading rate (OLR) are major factors in shaping the microbial community structure during the AD. The startup of anaerobic reactors is one of the most critical steps in the operation of



Source: Adapted from Ferry (2011) and Welander and Metcalf (2005).

Fig. 3.5 Biochemical pathways of Methanogenesis. Source: Adapted from Ferry (2011) and Welander and Metcalf (2005)

anaerobic systems, and the conditions applied during this phase will form the structure of the microbial community. Finally, anaerobic co-digestion has been used to improve the anaerobic digestion process with which the combination of different co-substrates is mixed to enhance biogas production.

3.4.1 Temperature and pH

Temperature and pH directly affect microbial growth and stability. Limited ranges of pH and temperature are related to the optimal bacterial growth rate, although their survival can occur with larger ranges (Speece 1983).

Variation in temperature during AD affects the stability of all microbial species due to their intracellular proteins that are thermostability dependent, particularly methanogens (Amani et al. 2010). In fact, temperature affects the development of the AD by influencing both the enzymatic reaction and the substrate diffusion rates, and methane formation is strongly temperature dependent (Gerardi 2003).

The ideal temperature levels related to AD are the mesophilic (25–40 °C) and thermophilic range (50–65 °C) in accordance with the optimal temperature range for the groups of microorganisms involved in the entire process (Ahring 1994; Metcalf and Eddy 2004). According to Chernicharo (2007), most of the anaerobic reactors have been designed and are operated in the mesophilic range, although thermophilic processes offer several potential advantages, such as an increase in microbial activity, and thus higher biogas production (Van Lier 2008). At the same time, at higher temperatures, thermodynamics for acetogenic conversions are more favorable, while a general decrease in microbial diversity can be observed, especially the complexity of the methanogenic community (Pap et al. 2015; Zábranská et al. 2000).

Moreover, the thermophilic microbial community is more susceptible to inhibition and sudden environmental changes than the mesophilic one. This inhibition is related to the lower growth yield of thermophilic microorganisms due to their higher decay rate, which is double that of mesophilic anaerobes (Wilson et al. 2008). At thermophilic conditions, the cells of the microorganisms show a tendency to lyse rapidly; also, higher energy is required for their maintenance and specific molecular properties of enzymatic reactions are necessary (Kim et al. 2002).

Several studies have demonstrated that acetogenic degradation of intermediate volatile acids, i.e., propionic and butyric acids, are better at thermophilic temperature due to favorable thermodynamics of syntrophic oxidation; however, methanogenic conversion of acetic acid has been more favorable at mesophilic conditions (Amani et al. 2015; Kim et al. 2002; Pap et al. 2015).

In recent years, due to advances in molecular biology, metagenomic and metabolomic techniques have led to new insights into anaerobic microbial populations in terms of diversity and activity at mesophilic and thermophilic temperatures. Notably, higher diversity of archaeal and bacterial communities is found at mesophilic temperatures, whereas the latter is considerably more diverse and dynamic than archaea at any temperature (Levén et al. 2007; Pycke et al. 2011). In addition, microbial diversity enhances the capability of the community to adapt

and respond to process instabilities, due to its ability of using parallel metabolic pathways (Ferguson et al. 2018).

Community analyses in anaerobic reactors showed the presence of bacteria affiliated with the phyla Chloroflexi, Synergistes, Bacteroidetes, Firmicutes, and Thermotogae in both meso- and thermophilic conditions (Chouari et al. 2005; Levén et al. 2007). Bacteroidetes and Spirochaetes were the dominating fermentative bacteria of the mesophilic processes while Thermotogae was the major group presented in thermophilic process (Hernon et al. 2006). The methanogenic archaeal community was commonly dominated by the phyla Euryarchaeota and Crenarchaeot; the acetoclastic methanogens from the genera *Methanosarcina* and *Methanosaeta* were dominant in the mesophilic reactor, and the Methanobacteriales species was abundant at thermophilic temperatures (Lee et al. 2017; Patil et al. 2010; Yu et al. 2014).

The pH is also an important factor in microbial growth and stability, and the ideal range has been reported to be 6.8–7.4 (Speece 1983). In addition, pH is intrinsically related to alkalinity and volatile acids, and these three environmental factors are equally important to the control the anaerobic processes (Chernicharo 2007).

Methanogens are extremely sensitive to pH, and these microorganisms have optimum growth in the pH range between 6.6 and 7.4; values above 8.3 and below 6.0 should be avoided due to their inhibition effect (Gerardi 2003). On the other hand, hydrolytic and acidogenic bacteria are generally less sensitive and can function in a larger range of pH (4.5–8.0); besides, even lower values can be supported (less than 4.5) (Lettinga et al. 1997). Due to the faster growth of acetogenic bacteria, volatile acids can accumulate if enough alkalinity is not provided (1000–3000 mg/L as $CaCO_3$) (Amani et al. 2010; de Aquino and Chernicharo 2005). Therefore, the control of pH aims to mainly reduce the risk of methanogenic inhibition by the low pH values.

3.4.2 Reactor Start-up

The properties of the microbial seed community regulate the rate of the reactor start-up whose duration can vary from a few days to even months. If the reactor start-up is not well developed, a long acclimation period can occur which leads to lower biogas production and poor reactor performance (Hickey et al. 1991). Furthermore, a short and successful start-up time is one of the key factors to economically improving the biogas production and increasing the competitiveness of anaerobic reactors (Weiland and Rozzi 1991).

During this initial phase, the hydrolytic and acidogenic bacteria groups dominate the system, especially because of their short generation time, which is highly active while the methanogenic microorganisms are just becoming established due to their low growth rate (Gerardi 2003; Weiland and Rozzi 1991).

The principal microbial factors that influence the start-up of the reactor are the dominating microbial groups, i.e., hydrolytic, acidogenic, acetogenic or methanogenic, growth rate and the shape of methanogenic community, the biomass

yield coefficient, and the rate adaption of the microorganisms to the substrate (Weiland and Rozzi 1991). Hence, start-up strategies should be developed to increase the population of the selected inoculum to improve the reactor performance and biogas production. These strategies include the control of fluctuations of external parameters such as temperature, hydraulic retention time (HRT), pH and OLR (Barber and Stuckey 1998).

The optimum temperature ranges are 33–37 °C and 50–55 °C for mesophilic and thermophilic inoculum, respectively (Kim et al. 2002). The pH of the substrate should be maintained in the range of 6.8–7.2 for the maximum methanogenic growth also to prevent accumulation of intermediate products such as VFA and ammonia (Angelidaki et al. 2006; Gerardi 2003). OLR must be as low as possible, and the optimal value depends on the reactor configuration and substrate composition (Barber and Stuckey 1999). Moreover, a long HRT during the initial period is recommended to avoid biomass washout (Leitão et al. 2006).

The seed inoculum used to start-up an anaerobic reactor is usually taken from another working reactor, especially an up-flow sludge bed reactor (UASB) or waste activated sludge, from a municipal digester or adapted from animal manure (Amani et al. 2010; Chachkhiani et al. 2004; Kobayashi et al. 2009). However, in some cases, start-up can rely on the internal inoculum available in the substrate by cultivating microorganisms throughout the anaerobic self-degradation (Kobayashi et al. 2009). According to De La Rubia et al. (2013), there is a relation between the high levels of *Archaea* microorganisms and the success of the reactor start-up; however, reactors that experienced a difficult start-up period had lower levels of *Archaea*. Therefore, the microbial community seed must contain a high level of methanogen microorganisms to optimize and reduce the start-up time.

3.4.3 Retention Time and OLR

Retention time and organic load rate (OLR) are parameters related to each other and to the reactor design and volume, flowrate and organic content of the feed, microbial growth rate and characteristics of the substrate, i.e., organic matter content.

In an anaerobic reactor, there are two retention times to considered: solids retention time (SRT) and hydraulic retention time (HRT). SRT is related to the average time that the microorganisms, i.e., solids, spend in the reactor while HRT is the time the substrates are in the reactor and is related to the reactor volume and influent flowrate (Chernicharo 2007). HRT can be used to control the dominant species in the reactor, whereas SRT is considered as an important factor that ensures the growth and stability of various populations of microorganisms inside the reactor (Kundu et al. 2017; Zhang and Noike 1994). The methanogens, due to their slow microbial growth rate, are the microorganisms that most affect the retention time of the operation.

From an economic point of view, short HRT is preferable due to a smaller reactor volume required, while high SRT maximizes the reactor performance, provides buffering capacity for protection against the shock loads and permits biological

acclimation to toxic compounds (Gerardi 2003; Weiland and Rozzi 1991). However, decreasing HRT usually leads to VFA accumulation which causes inhibition of methanogens and affects biogas production (Kuruti et al. 2017; Mao et al. 2015). Besides, shortening of SRT coupled with increasing OLR can lead to a higher biogas production rate and volumetric methane productivity, which improves the energy balance of the processes and overall degradation efficiency (De La Rubia et al. 2006; Nges and Liu 2010).

According to various recent studies using high-throughput sequencing and advanced molecular techniques, bacteria affiliated with the phyla Firmicutes and methanogens from the order Methanosarcinales, specifically *Methanosarcinaceae* group, were the dominant population at higher HRT, while at low HRT bacteria belonging to the phyla Gammaproteobacteria, Actinobacteria, Bacteroidetes, Deferribacteres, and archaea groups of Methanomicrobiales, Methanobacteriales, and Methanosaetaceae were predominant during the AD (Kundu et al. 2017; Wei et al. 2017; Xu et al. 2018c). At reduced SRT, Vanwonterghem et al. (2015) observed a washout of acetoclastic *Methanosaeta,* while the microbial community was dominated by bacteria from the genera *Alkaliflexus*, *Fibrobacter,* and *Ruminococcus.* By increasing the SRT from 4 to 12 hours, the authors detected the prevalence of populations belonging to the bacterial genera *Ruminococcus, Clostridium, Bacteroides*, and the archaeal genus *Methanosaeta.*

Methane production is particularly affected by the HRT, although HRT has been reported to cause less effects on microorganisms than OLR (Ferguson et al. 2018). During reactor start-up, OLR is preferably kept low and is gradually increased to trigger microbial growth along the operation which can lead to a higher methane production rate (Kundu et al. 2017). The stepwise increase in OLR allows the archaea community to adapt their cell density required for the consumption of VFA rapidly produced by the bacteria; hence, the methanogens are able to produce biogas constantly and attain a new steady state before a new increase in the OLR (Nakasaki et al. 2015).

In a study conducted by Rincón et al. (2008), the effect of OLR was investigated in a CSTR reactor and revealed that at low OLR, firmicutes, mostly represented by the genus *Clostridium,* were the predominant bacteria while the bacterial community which was most abundant at higher OLR were Pseudomonas, Actinobacteria, Bacteroidetes, and Deferribacteres. However, the archaeal community showed a static phylotypic composition mainly consisting of the *Methanosaeta* group as also demonstrated by Nakasaki et al. (2015). On the other hand, other studies showed a significant population shift from *Methanosaeta* to *Methanosarcina* groups by increasing OLR (Boonapatcharoen et al. 2007; Chelliapan et al. 2011).

OLR also influences the formation of anaerobic granular sludge in the high rate reactor, specially the UASB reactors (Hulshoff Pol et al. 2004). Mass transfer between incoming substrate and biomass, microbial proximity for syntrophic reactions, staging, and configuration of phased digesters are the key factors controlling the OLR (Amani et al. 2010). Therefore, the recommended value of OLR is greatly dependent on the type of waste, the operational temperature range, and reactor design.

Hydraulic and organic shock loads are caused by variations in HRT and OLR, respectively, and can result in a significant change in microbial community by altering the balance between the acidogenesis and methanogenesis, particularly affecting the archaeal community (Kundu et al. 2017; Vanwonterghem et al. 2015). The response of each syntrophic group to the change in conditional operations is related to their growth rate, and a proper balance between the different microbial groups is especially important to biogas production stability.

3.4.4 Anaerobic Co-digestion

Anaerobic co-digestion (AcoD) utilizes two or more substrates with complementary characteristics to balance the nutrients (C:N ratio), promote dilution of toxic compounds, improve synergism between microorganisms, and for the supplementation of trace elements and/or moisture. By combining co-substrates, AD of complementary residues can be maximized, resulting in higher biogas production, thus improving the economic viability of the AD process, promoting waste recycling, and contributing to environmental conservation (Mata-Alvarez et al. 2014).

Animal manure, sewage sludge, and organic fraction of municipal solid waste (OFMSW) are the most common residues utilized as the main substrate in AcoD (Beneragama et al. 2017; Elalami et al. 2019; Tyagi et al. 2018). Animal manure is usually complemented with agro-industrial wastewater, glycerol (glycerin), and cheese whey, while sewage sludge and OFSW are commonly utilized as co-substrates due to facilitated transportation logistics (Sosnowski et al. 2003). Other co-substrates include food waste, leachate, algae (macro and micro), industrial wastewater, fat, oil and grease (FOG), lignocellulosic biomass (yard waste and crop residues), and sewage (Esposito et al. 2012).

The characteristics and nutritional balance, especially the C:N ratio, of the co-substrates influence the stability between the bacteria and methanogen groups and can promote a more robust microbial community and enhance biogas production (Xu et al. 2018c). In fact, the ideal C:N ratio has been reported in the range of 20 to 35 (Puñal et al. 2000), and the combination of substrates to provide the optimal ratio is necessary to improve the biogas yield from AcoD. For instance, Rahman et al. (2017) reported the highest methane yield when a mixture between poultry wastewater and lignocellulosic biomass had a C:N of 32; (Haider et al. 2015), who co-digested food waste and rice husk, showed that feedstock C:N ratio of 20 promoted the best AcoD performance, while Astals et al. (2011) found an optimum C:N ratio of 23 treating pig manure and glycerin.

Moreover, the microbial community structure is also a major factor in the performance of AcoD. The bacterial community is capable of metabolizing a large variety of substrates although feedstock composition regulates the bacterial consortia diversity, thus influencing the archaeal community (Ros et al. 2013). Bacteria affiliated with the Firmicutes and Chloroflexi groups have been found in a wide range of AcoD processes due to their capacity of degrading a large amount of organic waste (Chouari et al. 2005; Tyagi et al. 2018). Specifically, in AcoD using

animal manure as the main substrate, pyrosequencing results revealed the presence of *Halothermothrix*, *Selenomonas*, and *Halocella* affiliated to Firmicutes and *Methanosarcina* species of the family *Methanosarcinaceae* (Goberna et al. 2010; Riya et al. 2016).

AcoD of sewage sludge with OFMSW, both major urban environmental issues, have been reported to be a sustainable method for disposing of this waste (Edwards et al. 2017). 16S rRNA gene sequences revealed in co-digestion of sewage sludge and urban OFMSW that *Thermonema* was dominant bacteria, while other bacteria belonging to phyla Firmicutes, Bacteroidetes, Synergistes and Thermotoga, particularly the orders *Clostridiales, Bacteroidales, Thermoanaerobacterales, Synergistia* and *Thermotogales* were detected in small amounts; archaeal assigned to the orders Methanobacteriales, Methanomicrobiales, and Methanosarcinales were the predominant methanogens (Fitamo et al. 2017; Martín-González et al. 2011).

Bacteria associated with the phylum Firmicutes and Bacteroidetes, particularly *Clostridia* and *Bacteroidia* species, were reported to be the most abundant microorganisms in AcoD of agricultural waste combined with animal manure (Ziganshin et al. 2013). The facultative acetoclastic *Methanosarcina* genus, the strict acetotrophic genera *Methanosaeta*, the hydrogenotrophic genera *Methanocalculus, Methanobacterium, Methanolobus, Methanoculleus, Methanothermobacter, Methanobrevibacter, Methanocorpusculum, Methanomicrobium,* and *Methanospirillum* and the methanol-consuming genus *Methanosphaera* were detected with the AnaeroChip microarray in the AcoD of cattle manure and olive mill waste, showing the diversity of archaeal during co-digestion (Goberna et al. 2010).

3.5 Process Configurations for Biogas Production: From Consolidated Technologies to Innovations

Several anaerobic digestion technologies have been proposed over the years, and the way they are implemented around the world can vary significantly. In developing countries, there are many small-scale household digesters that produce enough biogas to be used in the home, while large-scale agricultural or centralized digesters with large capacities are found in developed countries. Currently, there are 132,000 biogas digesters in operation worldwide, most of them in China, Europe, and United States, where there are over 100,000, 18,202, and 2200 units, respectively (EBA 2019; REN21 2020).

Biogas plants can be separated into three broad categories: micro-digesters using the biogas, scale digesters, which generate electricity and produce upgraded biogas, i.e., biomethane, respectively (World Biogas Association 2019). From an economic point of view, AD systems can be classified into two categories: large-scale AD systems, largely used in sewage plants and wastewater industrial units, and small-scale AD systems, such as households and community scale farms in rural areas (Vasco-Correa et al. 2018).

Likewise, anaerobic systems generally used to treat waste can be separated into two main groups: conventional systems, such as sludge digesters, septic tanks, and anaerobic ponds; and high-rate systems, such as up-flow sludge blanket reactors (UASB), expanded granular bed reactors (EGSB) and an anaerobic sequencing batch reactor (ASBR) (Chernicharo 2007). However, anaerobic processes can be classified according to the solids concentration in the reactor: wet or dry (or solid state) AD processes, whose reactors are operated with solids content below 10% and between 15% and 35%, respectively (Weiland 2010).

Currently, certain reactor configurations are very well established and are considered consolidated technologies, which are used in several industrial and agricultural units. However, new types of reactors have been proposed to enhance biogas production to provide diverse environment for different microbial populations and to control factors of inhibition. Recent research focuses on novel reactor geometry and design as well as two-phase reactors.

3.5.1 Consolidated Technologies

Among the consolidated technologies utilized in the AD, the high-rate systems transformed the AD into a commercial and sustainable process which was successfully applied to treat various types of wastewater and residues along with the bioenergy production. Developing high-rate reactors allowed the separation of HRT and SRT, leading to smaller reactor volumes by reducing the HRT applied while high biomass concentration enhances the reactor performance (Lettinga et al. 1997).

High-rate anaerobic reactors can be classified according to the type of biomass growth in the system: suspended (or dispersed) growth, whose microorganisms are present as flocs or granules, and attached growth, which requires a moving or fixed inert support material for the microbial fixation, promoting the formation of biofilms (Chernicharo 2007). Anaerobic filters, expanded/fluidized bed reactor, and the anaerobic membrane reactor are the most commonly known reactors with attached microbial growth while granular sludge is seeded and/or developed in UASB, expanded bed reactors such as EGSB and anaerobic reactor with internal recirculation (IC) (Van Lier 2008).

Among the high-rate reactors, the UASB is certainly the main process configuration in current use. The granulation of anaerobic sludge has been considered the major reason of successfully implementing UASB reactors for AD treatment of several kinds of waste, particularly in domestic sewage treatment (Foresti et al. 2006). The granule is formed by microorganisms that organize themselves into dense and highly structured aggregates, in which a diverse microbial community grows in a syntrophic symbiosis (Liu et al. 2002). The granule structure mainly consists of different layers with the hydrolytic/acidogenic bacteria primarily dominating the outer layer and the inner layer consisting of methanogens (Tartakovsky and Guiot 1997).

Besides years of research, the mechanisms of granule formation are still not fully elucidated; however, it seems that the process is a spontaneous microbial involvement (Show et al. 2020). Theories approaching the physical, microbial, and thermodynamic conditions applied to the anaerobic system have been considered the major factors responsible for granulation. According to Hulshoff Pol et al. (2004), *Methanosaeta concilii* is a key microorganism in anaerobic granule formation. The Cape Town hypothesis stated that granulation depends on *Methanobacterium* strain AZ while the Spaghetti Theory proposed that granule formation can be initiated by the attachment of filamentous *Methanosaeta* on a precursor whose granule microbial structure is further developed by incorporating other microorganisms such as *Methanosarcina* (Hulshoff Pol et al. 2004; Show et al. 2020).

Other consolidated configurations widely used in AD plants are continuously stirred tank reactors (CSTR), in which the microorganisms are suspended inside the reactor through intermittent or continuous mixing; and the expanded bed reactors (EGSB), which are similar to UASBs except that the high hydraulic rate expands the sludge, intensifying the hydraulic mixture providing greater contact between the biomass-substrate. (Mao et al. 2015; Seghezzo et al. 1998).

Regardless of the small-scale AD systems, mostly are household units (2–10 m^3), usually located in rural areas in China, India, and other developing countries. There are three types of digesters commonly used: the Chinese fixed dome digester, the Indian floating drum digester, and the tube digester (Surendra et al. 2014; Vasco-Correa et al. 2018). These digesters have a simple design, low-cost installation, and the biogas produced is usually used for cooking and heating.

3.5.2 Innovation

Many studies have focused on developing new anaerobic reactor configurations and/or redesigning the existing models to enhance biogas production, yield and quality, and to optimize and economically improve AD. Multi and two-phase AD systems have been used to optimize the AD by separating hydrolysis/acidogenesis and acetogenesis/methanogenesis phases. These systems can utilize two (or more) separated reactors or only one integrated reactor in which the AD phases can be physically separated, such as the anaerobic baffled reactor (ABR) (Ke et al. 2005; Rajendran et al. 2020).

Anaerobic membrane bioreactors (AnMBR) are considered as new-generation technology, whose process can effectively retain key microorganisms such as methanogens allowing high biomass concentration while obtaining a high-quality effluent (Zhen et al. 2019). Various reactor configurations have been developed over the years, such as anaerobic fluidized-bed membrane bioreactors, anaerobic submerged rotating membrane bioreactors (AnSRMBR), anaerobic dynamic membrane bioreactors (AnDMBR), and anaerobic electrochemical membrane bioreactors (AnEMBR) (Maaz et al. 2019). However, there are some challenging aspects that must be overcome to consolidate the use of membrane technology on a large scale,

such as membrane fouling and recovery of dissolved methane (Smith et al. 2012; Vinardell et al. 2020).

The quality of the final effluent of the AD process is a constant concern in wastewater treatment plants. To overcome this issue, the combination of anaerobic and aerobic systems has been used in industrial wastewater treatment for years, particularly the food industry. However, new process configurations are being widely studied to reduce costs and improve the quality of the effluent in order to meet the regulatory regulations for disposal, in addition to increasing bioenergy recovery. The combination of anaerobic and aerobic processes in a single integrated reactor is attractive in the sense of meeting the constraints related to space, odor, and minimal sludge production and at the same time, presenting an excellent cost–benefit ratio. However, most integrated systems reported in the literature lack large-scale implementation (Chan et al. 2009).

3.5.3 Solid-state Anaerobic Digestion

Solid-state anaerobic digestion (SS-AD) englobes the biogas production from various solid wastes, such as waste activated sludge, lignocellulosic biomass, and municipal solid waste. The process is usually operated at a total solids (TS) concentration between 15% and 50% and has the potential to provide, besides the biogas, organic fertilizer (soil conditioner) or carrier material for biofertilizers and pelletized fuel (Van Lier et al. 2001).

SS-AD systems have some advantages over liquid AD such as lower energy requirements for heating and mixing, fewer moving parts, absence of floating and stratification of fats and fibers, minimal material handling, and a greater acceptance of inputs containing glass, plastics and grit (Li et al. 2011; Mata-Alvarez et al. 2000). However, AD of solid waste requires longer retention times due to slower mass transportation, which were reported to be up to three times longer than liquid AD (Khalid et al. 2011).

Several reactor configurations, continuous or batch modes, have been utilized for SS-AD. The start-up of SS-AD reactors has been considered as a critical phase, which requires a highly concentrated and active inoculum to improve digestion time and efficacy during the initial phase of operation (Forster-Carneiro et al. 2008). Moreover, the temperature regulates the performance of SS-AD as well as the selection of waste/inoculum and feedstock/effluent ratios and the assessment of anaerobic biodegradability of the waste (Mata-Alvarez et al. 2000).

Nevertheless, there are some issues associated with SS-AD such as lower methane yield and organic matter stabilization and, to overcome them, anaerobic co-digestion has been proposed to enhance biogas production and yield as well as to produce a stabilized compost to be recycled as an organic amendment (Van Lier et al. 2001). Moreover, pretreatment of the substrates can be used to improve the performance of SS-AD by breaking down the complex organic structure into simpler molecules that are easily degraded by the microbial community (Yadvika et al. 2004).

During AD of solid wastes, hydrolysis is considered a major rate-limited phase which influences the conversion efficiency of the process. Regardless of the microbial community in SS-AD, hydrolytic bacteria Firmicutes and *Clostridium* species are most commonly found, while *Clostridiaceae* are microbial community that are responsible for degrading the particulate COD of solid residues (Regueiro et al. 2014). *Thermomonospora, Tepidimicrobium, Pseudomonas, Acinetobacter, Ralstonia, Lactobacillus* and *Shewanella* have been reported to be involved in the degradation of food waste and municipal solid waste (Shi et al. 2020; Wu et al. 2020). The cellulolytic bacteria such as *Ruminococcus Clostridium, Cellulomonas*, *Thermomonospora, Baceriodes, Erwinia, Acetovibrio, Bacillus, and Microbispora* are related to the degradation of lignocellulosic biomass due to their production of cellulases (Heeg et al. 2014; Lo et al. 2009).

A pyrosequencing-based metagenomic study demonstrated that species affiliated to genera *Methanosarcina, Methanosaeta* and *Methanoculleus* of Euryarchaeota, specifically the species *Methanosarcina barkeri fusaro, Methanoculleus marisnigri JR1,* and *Methanosaeta theromphila* consisted of the main methane-producing microbial community in an SS-AD reactor (Li et al. 2013).

Therefore, SS-AD systems may have a high diversity of micro-environments due to the heterogeneous nature of the feedstock. This diversity allows the growth of the microbial groups necessary to complete the first steps of AD, thus providing conditions to establish methanogens.

3.6 Conclusion and Future Perspectives

AD is a well-established biological route, commonly used for biogas production and consists of a four-step process that involves the action of different groups of microorganisms. Currently, different materials can be used as feedstock. It is particularly important to study the composition and physical-chemical structure of each substrate. Moreover, the optimal feedstock choice is necessary to plan the adequate technological model for the effective construction of the biogas plant.

Besides the type of substrate, it is necessary to understand the syntrophic activity of the microbial communities involved in the AD. Once knowing the present microbiota, the nutritional and operational conditions can be used to improve the biomethane production. For instance, the major microorganisms presented in the four-steps are: the microbial degradation in the hydrolysis and acidogenesis steps involve the phylum Firmicutes, from genera *Anaeromusa, Anaerosphaera, Aminobacterium, Aminomonas, Gelria, Peptoniphilus, Thermanaerovibrio, Clostridium, Proteiniborus* and *Sporanaerobacter.* The microbial degradation in the acetogenesis step involves acetogenic bacteria from the genera *Clostridium* and *Acetobacterium.* The last step of the AD, considered the limiting phase, involves methanogenic archaeal microorganisms that are the mainly responsible for producing methane and belong to the phylum Euryarchaeota.

The published data for AD indicate that several factors such as temperature, pH and OLR can affect the stability of the microbial community on anaerobic systems,

resulting in high or low biogas rates. Therefore, optimization conditions such as temperature levels (25–40 °C), pH range of 6.8–7.4, short HRT, high SRT maximize reactor performance, provide buffering capacity for protection against the shock loads and permits biological acclimation to toxic compounds. In addition, recent studies claim that advances on molecular biology, metagenomic and metabolomic techniques led to new insights into anaerobic microbial populations in terms of diversity and activity at mesophilic and thermophilic temperatures.

The main microbial factors that influence the start-up of the reactor are the dominating microbial groups, i.e., hydrolytic, acidogenic, acetogenic or methanogenic, growth rate and the dominating shape of the methanogenic community, the biomass yield coefficient, and the rate adaption of the microorganisms to the substrate. Finally, anaerobic co-digestion has been used to improve the anaerobic digestion process in which the combination of different co-substrates is mixed to enhance biogas production mainly due to the equilibration of the nutrients balance in the mixture (C:N ratio).

High-rate systems include reactor configurations, which are well-established and consolidated technologies, which are used in various industrial or agricultural plants. However, novel types of reactors have been studied to provide diverse environment for different microbial populations and to control factors of inhibition. Different solutions in terms of reactor configurations, such as the development of new anaerobic reactor configurations and/or redesign of the existing models are applied to enhance biogas production. For example, two-phase reactors to separate the hydrolysis/acidogenesis and acetogenesis/methanogenesis phases. Besides, the solid-state anaerobic digestion (SS-AD) approach not only englobes the biogas production from various solids waste, but also has the potential to provide organic fertilizer or carrier material for biofertilizers and pelletized fuel.

AD is an efficient and consolidated technology used worldwide to convert different types of wastes, residues, and wastewaters to a highly energetic biogas. The biogas produced in AD processes can be used to generate electricity and heat and be upgraded to biomethane, by removing CO_2 and other impurities, rather than being injected to natural gas pipelines or used directly as vehicle fuel. Despite using biogas as a source of renewable energy, the AD process is involved in climate change mitigation; by reducing greenhouse gas emissions and capturing biogas of landfills; improving urban air and water quality by substituting fossil fuel to biomethane and promoting sanitation, respectively. Moreover, biogas generation contributes towards a circular economy, transforming waste and residues into bioenergy, as well as improving food security whose inorganic fertilizers can be replaced by biofertilizers.

Although there are numerous advantages by utilizing bioenergy from AD, the biogas industry is in its initial stages of development. According to the World Biogas Association (2019), only 1.6–2.2% of the full potential of AD is reached and to fulfill the full potential of biogas, policies such as waste management and comprehensive agricultural policies; regulations are also required to encourage the implementation of AD technology. In addition, incentives that favor biogas over oil and fossil fuels,

such as tax exemptions and tax credit, credits for carbon reduction and carbon trading, as well as tax cuts for domestic and small-scale digesters.

However, biogas production has been growing in the European energy market where the number of biogas plants has increased continuously over the past years, especially due to numerous incentives from the government and European Union which includes the obligation certification for energy renewability and taxes policies. Biogas generation and utilization are also representative in China and India although they are restricted to small-scale units and concentrated in rural areas. The United States has the second highest national bio-power capacity and generation; however, the biogas market is stagnant in the country due to the lack of policy drivers and incentives. In Latin American countries such as Brazil, there are over 300 large-scale biogas plants in operation where more than three million cubic meters of biogas are produced daily, to generate electricity and biomethane (CIBIOGÁS - Centro Internacional de Energias Renováveis - Biogás 2019; EBA 2019; REN21 2020).

AD can be considered an industry global growth potential that generated high-value products. The potential of biogas production is high and can be a sustainable option to substitute fossil fuels. Governments must propose new regulations and incentives that favor AD, as well as waste management alternatives. In fact, AD technology allows the action of microorganisms and a key factor to economically improving the AD is to better understand the syntrophic metabolism that occurs throughout in each step of the microbial degradation, as well as the bacteria and archaea microorganisms involved in the processes.

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