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Volatile fatty acids in ruminants and their role as feed additives: a review

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ABSTRACT

Ruminants, as an inseparable part of the food chain, will play a determining role in meeting future food demands and guaranteeing global food security for the ever-growing population. In this regard, supplying ruminants with feed material and feed additives that enhance animal health and products has attracted great research interest in the field of ruminant nutrition. Volatile fatty acids (VFAs), such as acetic, propionic and butyric acids, which are endogenously generated in the rumen, are mainly responsible for providing the animal with metabolizable energy and as precursors for animal products. In addition, VFA can be supplied to ruminants as *ex situ* additives. Extensive research on VFA additives has proven that VFA supplementation affects the development of ruminant gastrointestinal tract, hormone levels, milk yield and composition, adipose tissue, meat quality, weight gain, dry matter intake, etc. The current review provides a unique collection of studies on the effects of VFA additives on ruminants in addition to an in-depth overview of the ruminant digestion system and the fate of different fractions of feed material. Moreover, the potential for sustainable provision of VFA additives from organic-rich waste and residues through anaerobic digestion plus post separation and concentration is critically discussed in this review.

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1 Introduction

As projected, a population of more than 9.5 billion people will reside on planet Earth by 2050. This large population will have greater food demands, stressing global food markets and in turn imposing burdens on food provision sectors such as the livestock agricultural sector, pushing them to new production limits (UN 2019). In this context, among livestock, ruminants, such as cattle, sheep, goats, etc. and their products will be playing a pivotal role in the food chain. Between 2015 and 2019, the global population of cattle, sheep and goats increased from 3.63 to 3.83 billion (Michalak et al. 2021). In the EU alone, there were 151 million bovine animals, sheep and goats in 2019, providing around 7.4 million tons of meat to the food market (Union 2020). Ruminant production intensification requires an extended supply of feed material and additives not only to maintain but also to increase animal productivity, welfare and health (Michalak et al. 2021). However, considering the land usage for animal feed production (about 30% of total arable land (Steinfeld et al. 2006)), the water footprint of livestock production (about 29% of water used in agricultural activities) (Mekonnen and Hoekstra 2011) in addition to the projections on cereal demand in the animal feed sector by 2050 (about 25% total global cereal production) (FAO 2018), maintaining such balance may seem difficult to achieve through conventional feed provision practices.

Taking such concerns into account FAO has provided a thorough report on how to transform the livestock sector to comply with the Sustainable Development Goals (SDGs) set by the United Nations General Assembly in 2015 (FAO 2018). In this context, the provision of ruminant feed components and feed additives should involve sustainable environmental, social and economic practices to guarantee a long-

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term healthy dynamic relationship between agricultural sector prosperity and human food provision. The importance of sustainable approaches for ruminant feed provision becomes more pronounced when its contribution to boosting agricultural development, providing food security and reducing poverty is taken into consideration (Bank 2020).

One way to contribute to the production of more from less in the livestock sector is to supply ruminant feed with additives. Ruminant feed additives are supplemented in the diet to increase animal health, feed utilization and metabolism, and productivity through boosting animals' health and yield of animal products and to benefit from their pre- and probiotic effects on the rumen and gut microflora. One of the extensively explored classes of ruminant feed additives is volatile fatty acids (VFAs), such as acetic, butyric and propionic acids. VFAs are natural metabolites generated in the rumen of ruminant due to microbial bioconversion of feedstuff (Allen 1997). The role of ruminal VFAs in the provision of metabolizable energy and precursors for animal products was revealed in the 1940s (Orskov et al. 1979).

The feedstuff ingested by ruminants contains mainly carbohydrates, lipids, proteins and minerals (Figure 1). Carbohydrates such as sugars, starch and lignocellulosic material, which are abundant in plant-based diets, are the main compounds that are converted by rumen microorganisms to VFAs and gases such as carbon dioxide and methane (Moran 2005; Nozière et al. 2010). The VFAs produced in the rumen are generally absorbed by the rumen walls and transported to the liver through the bloodstream to be converted to energy sources or other valuable biochemical units (Kleiber et al. 1954; Aiello et al. 1989; Bergman 1990; Seal 1993). Decades of scientific findings in the field of ruminant nutrition have revealed the diverse roles attributed to VFAs in the ruminant body. In this context, VFAs are proven to contribute to energy provision, weight gain, gastrointestinal tract development, milk yield and composition (fat, protein, etc.), changes in hormone levels, the composition and content of adipose tissue, meat quality, microbial distribution in the rumen microflora and other factors (detailed description in Section 3).

Considering the major role that VFAs play in ruminant wellbeing and products, *ex situ* supplementation of VFAs in ruminant diets has been extensively studied to better understand the mechanisms responsible for the effects observed and to be able to enhance animal health and product yield and quality by harvesting the potentials in the added VFAs. The supplementation of VFAs in liquid solutions or dry salt forms to ruminants' diets along with dry matter or by infusion at different sites has been researched by animal nutritionists since the 1950s (Klerutia et al. 1954; Martin et al. 1959; Sander et al. 1959) to the date (Urrutia et al. 2019; Fukumori et al. 2020; Gheller et al. 2020). However, if VFA supplementation in the ruminant diet assists in the sustainable growth of the livestock sector to meet future market demands and focuses on less resource input and more animal product output, additive VFAs should be provided from a renewable low-value source produced in an environmentally friendly and economically feasible practice.

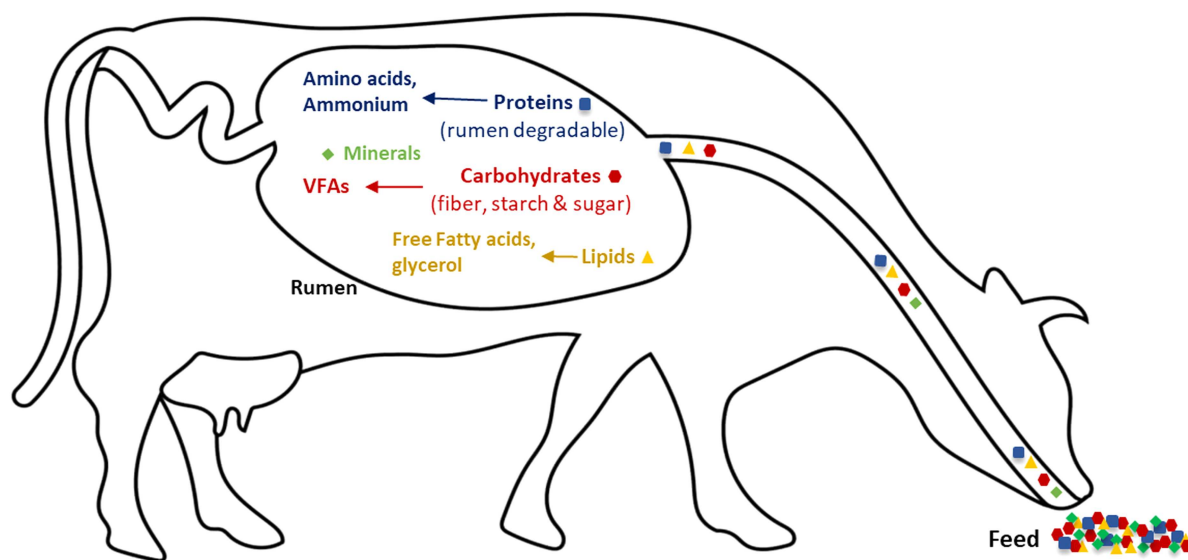


Figure 1. General schematic on different fractions of ruminant feed and their fate in the rumen.

In anaerobic digestion (AD), a process well-known as an organic waste management approach used for the conversion of organic-rich waste and residual streams to biogas, VFAs are generated as intermediate products. An anaerobic digester functions similarly to the rumen, where organic matter is digested by a symbiosis of a mixture of different microorganisms. During AD, if the stage responsible for the conversion of VFAs to methane is disturbed, VFAs can accumulate and recover for other applications, such as ruminant feed additive. The AD effluent rich in VFAs cannot be directly applied as a feed additive, as it contains particulate matter, unwanted microorganisms and impurity compounds (ammonium, etc.). In this regard, a spectrum of separation and concentration techniques, such as membrane filtration, adsorption, solvent extraction, distillation, etc. have been studied to clean, polish and upgrade VFA streams from the AD process. Considering the maturity and robustness of the AD process and the flexibility of VFA separation and purification techniques, meeting the demands for sustainable VFA production for ruminant feed supplementation through residue- or waste-derived VFAs can introduce new horizons in feed additive provision that comply fully with a circular economy.

This review presents a unique and rather complete collection of scientific findings on the production of VFAs in the rumen, the fate of different VFAs in the ruminant body, the effects of VFA supplementation on ruminant health and products and sustainable approaches for the production and recovery of VFA additives from organic residues. Moreover, for better understanding of feed digestion in ruminants, the ruminant digestive tract, feed components and their digestion procedure and products, plus the composition of rumen microorganisms, are thoroughly described. Above all, a critical review has been developed arguing the potentials of production of VFA additives from anaerobic digestion of organic waste and residues, in addition to the techniques used for VFA effluent post-treatment and upgrading.

2 Digestion in ruminants

Ruminants consume different plants, such as forages and cereals. Plant cell walls are made of complex polysaccharides, almost solely cellulose, hemi-cellulose, lignin and pectin (Ribeiro et al. 2016). Among livestock, ruminants are unique in evolving a forestomach, the rumen, where enzymes are produced in symbiosis with the rumen microbiota. The complex microbiota includes bacteria, protozoa, fungi, archaea and viruses. These microbes, with their substrate-specific enzymes, have the capacity to efficiently convert plant cell wall carbohydrates via VFAs and microbial proteins into high-quality products such as meat and milk (Morgavi et al. 2013).

Ruminants have three other stomach compartments besides the rumen: the reticulum, omasum and abomasum. Newborn calves have an incompletely developed rumen, both physically and metabolically (Warner et al. 1956). When the rumen is developed, ruminants live in symbiosis with their rumen microbes. This symbiosis gives the ability to digest plant polysaccharides that humans are not able to do, thus making no competition for those feeds between ruminants and humans (Hungate 1966).¹ Rumen microbiota are provided with nutrients and desirable surroundings from the ruminant, and the microbes provide the host animal with VFAs, B vitamins and microbial proteins through the digestive enzymes produced by the microbes (Nagaraja 2019).

2.1 The digestive tract

2.1.1 Saliva

During evolution, the rumen microbiota has adapted to live at a temperature of 38 °C–40 °C and an anaerobic environment with a pH between 5.5 and 7.0 (Hungate 1966). The rumen experiences diurnal pH fluctuations due to decreases in pH after feeding and increases in pH during rumination (Allen 1997). Furthermore, pH also fluctuates due to feed intake, type of feed and feeding strategy (Zebeli et al. 2008). Therefore, saliva secretion during chewing is important to act as a buffer in the digestive system. When ruminants chew, saliva mixes with the feed stuff and forms a bolus. Saliva contains bicarbonate and phosphate ions, which remove hydrogen ions from rumen fluid by alkalization (Allen 1997). It is important to minimize diurnal pH fluctuations to achieve optimal microbial degradation of the feed, which is accomplished by having free access to a well-composed diet 24 h per day. The amount of saliva produced is dependent on the total chewing time, including eating and rumination time, which are affected by the

characteristics of the feed stuff, such as fibre content, hardness and particle size (Nørgaard et al. 2011; Volden 2011). Ruminants fed grains have less saliva production than animals fed a forage-rich diet (Krehbiel 2014).

2.1.2 Reticulum and rumen

Feed stuff swallowed ends up in the rumen. Depending on the particle density, feed will float in the liquid phase or sink in the ruminal fluid (Krehbiel 2014). The rumen consists of different layers, in the top is a layer of gas, below a floating mat of particles and ruminal fluid phases exist with different densities under the mat. The mat has a lower density than water does and can float on top of the liquid layer. The floating mat consists of larger and less dense feed particles, which are less fermented and will be ruminated again. The floating mat is important because the content of larger particles in the floating mat stimulates rumen wall contraction and rumination. Forage fibres that are degraded slowly in the rumen can thereby contribute to longer rumen retention times and stabilize the pH of the rumen. Fermentation is intensive in the intermediary zone, which is the layer between the floating mat and the ruminal fluid. Depending on feed stuff, density of the ruminal fluid differs (Tafaj et al. 2004).

Reticulum and rumen are joined by a fold of tissue and are often discussed as one part—reticulorumen. The reticulum has a unique honeycomb structure in which the epithelial tissue is formed on 4, 5 or 6 sides. The honeycomb structures represent small papillae. Nevertheless, the rumen does not contain honeycomb structures but rather a large number of papillae of various shapes and sizes. Rumen papillae are finger-like projections covering the interior of the rumen wall surface that play an important role in ruminal volatile fatty acid uptake through absorption. The main factors defining ruminal papillae size are said to be food intake, the ruminal fermentation rate and the weight of the rumen digesta (Moon and Campbell 1973; Amaral et al. 2005; Clauss et al. 2009; Roth et al. 2009). Papillae, with their highly absorptive surfaces, allow the movement of solutes able to traverse the epithelial cells separating the stomach contents from the blood supply (Krehbiel 2014). In addition, an increase in papillae size enhances rumen efficiency by increasing the available rumen surface area (Gaebel et al. 1987; Bannink et al. 2008).

2.1.3 Rumen contraction and rumination

The unique characteristic of ruminants is rumination. During rumination, digesta from the rumen is regurgitated, regurgitated liquids swallowed, remasticated, and reingested and the bolus is reswallowed (Ruckebush 1988). The reticulorumen has tension receptors that are activated by mild tactile stimulation and low to moderate distension of the rumen by ruminal contents. The activation of tension receptors stimulates rumination. Nevertheless, a large distension of the rumen (e.g. bloat) or various chemical stimuli, e.g. high concentrations of VFAs, inhibit ruminal contractions (Ash and Kay 1959). During rumination, chewing is slower and steadier compared to eating. Moreover, during rumination, digesta from the reticulum are regurgitated through the cardia, into the oesophagus and then into the mouth. Depending on the fibrous content, there is a physiological maximum rumination time (De Boever et al. 1990). Chewing and ruminating reduce the particle size of feed and allow the complex polysaccharides to be colonized and digested by the rumen microbiota. The degradation of feedstuff can be divided into different parts. After the feed particles are damaged by chewing and rumination and their inner structure becomes exposed, the process of hydrolyzing the complex structural material via microbial enzymes starts (Huws et al. 2013). As the feed is ruminated, the particle size is further reduced, and the gravity increases. When a particle has a specific gravity, it tends to sediment. Contractions in the rumen push the digesta, which are eligible for passage out of the rumen, towards the reticulum and eventually into the omasum (Ruckebush 1988).

The chewing promotes regular, strong mixing contractions that help the digesta move into different compartments in the rumen. This movement of the digesta helps the end products of digestion reach the right position near the epithelium for absorption. Furthermore, the contractions move bicarbonate into the ruminal content. Reticulorumen contractions are also important for the eructation of gas from the rumen. Finally, those contractions are responsible for moving high-density particles at the bottom of the rumen, microbial cells and liquids into the omasum (Okine et al. 1989).

2.1.4 Omasum and abomasum

The omasum, the third chamber in the digestion tract of a ruminant, is filled with folds of various sizes that make water absorption efficient. Besides water, Na^+ , K^+ and some VFAs are absorbed (Krehbiel 2014). Different species of ruminants have smaller or larger omasum due to body weight and diets where grazing ruminants have a larger omasum compared to browsing animals do (Clauss et al. 2006). The abomasum follows the omasum and is different from the previous three, due to its enzymatic degradation compared to microbial degradation in the rumen and reticulum. The abomasum is similar to what is found in the digestion tract of non-ruminant animal, and has a low pH and contains secretory tissue that produces mucus, pepsinogen and HCl (Krehbiel 2014). The entering digesta includes some microbes, undigested fibre, but also proteins and some sugars produced by microbes. Nutrients, such as bypass protein, fat and carbohydrates not digested in the rumen, may be digested in the abomasum or in the intestine.

2.1.5 Intestine

In the abomasum, the digesta enters the intestine, where the digestion is similar to that of non-ruminants. Enzymes are secreted from the pancreas and enter the intestine to digest proteins, sugars and starch. From the gall bladder, bile is produced to digest fats. Although enzymes are produced in the intestine to aid digestion, their major function is to absorb digested nutrients. Most of the nutrients are absorbed in the intestine, except VFAs, which are absorbed in the rumen. When the digesta enters the colon, water is absorbed and undigested feed, some excess water and metabolic wastes leave the ruminant as faecal material (McDonald et al. 2011).

2.2 Rumen microflora

Ruminants depend on diverse symbiotic microbiota, bacteria, archaea, protozoa, fungi and viruses—to ferment plant material in the rumen. These microorganisms inhabit the rumen fluid, feed particles and epithelium (Cho et al. 2006) and provide the host with VFAs, microbial protein and B vitamins (Nagaraja 2019). The microbial composition is dynamic and influenced by diet and the rumen environment, which in turn affects fermentation end products (De Menezes et al. 2011; Henderson et al. 2015). Forage-rich diets support higher microbial diversity than concentrate-rich diets do (Tapio et al. 2017).

Bacteria: Bacteria are the dominant group (up to 10^{11} cells/ml) (Morgavi et al. 2013) and occur in fluid-, solid- and epithelium-associated fractions (Nagaraja 2019). They possess enzymes such as cellulases, amylases, proteases and lipases, enabling the digestion of structural and nonstructural carbohydrates and the production of VFAs, lactate, CO_2 and H_2 as end products (Nagaraja 2019; Krehbiel 2014).

Protozoa: Protozoa (10^4 – 10^6 cells/ml) (Morgavi et al. 2013) contribute to fibre and protein degradation and recycle nitrogen by ingesting bacteria (Nagaraja 2019). By rapidly consuming starch, they can moderate the fermentation rate and help prevent rumen acidosis in high-grain diets (Newbold et al. 2015).

Fungi: Anaerobic fungi (10^3 – 10^6 zoospores/ml) (Morgavi et al. 2013) initiate fibre breakdown by penetrating plant tissues via zoospores and rhizoids (Lowe et al. 1987; Edwards et al. 2008; Belanche et al. 2012). They often act syntrophically with methanogens, enhancing fibre degradation and contributing to methane formation (Nagaraja 2019).

Archaea: Archaea (10^6 cells/ml) (Morgavi et al. 2013) are responsible for methanogenesis, using H_2 to reduce CO_2 to CH_4 (Wang et al. 2017). Efficient H_2 removal supports stable rumen fermentation and VFA production (Janssen and Kirs 2008).

Viruses: The rumen virome (10^7 – 10^{10} particles/ml) (Morgavi et al. 2013) consists mainly of bacteriophages, which infect bacteria but may also target protozoa, fungi and methanogenic archaea (Gilbert et al. 2020). Viral lysis contributes to microbial turnover and may release enzymes that enhance extracellular feed degradation. Viruses are also thought to influence microbial population dynamics and gene exchange (Adams et al. 1966; Hoogenraad et al. 1967; Gilbert et al. 2020).

2.3 Carbohydrate digestion

The ruminant diet can be composed of different lipids, proteins and carbohydrates that are taken in by the animal, digested and converted to products such as VFAs, ammonium, microbial biomass and more.

Carbohydrates, which are specifically plentiful in plant biomass-based diets (around 65%–75%), are the main precursors for the ruminal fermentation of VFAs, mainly acetic acid (AcA), propionic acid (PrA) and butyric acid (BuA), and gases such as carbon dioxide and methane (Moran 2005; Nozière et al. 2010). This occurs as the ruminal microbial community breaks carbohydrates (enzymatic hydrolysis) into smaller saccharides. Small sugars are then utilized by microorganisms and used as energy and carbon sources for microbial growth and metabolite formation (Sutton 1971). Based on the type of carbohydrate, their digestion rate by ruminal microbes differ, for example, sugars and starch are digested faster than plant cell wall components such as cellulose (Moran 2005).

Lignocellulosic materials contain digestible structural carbohydrates such as cellulose and hemicellulose. However, the digestion of these structural carbohydrates is rather slow, as the recalcitrant structure of lignocelluloses and the crystallinity of cellulose hinder enzyme accessibility, activity and effectiveness. Specific bacteria are responsible for the breakdown and conversion of these structural carbohydrates to VFAs. However, these bacteria are sensitive to rumen acidity and dietary fat content. Therefore, if the pH of the rumen decreases due to the high dietary content of lipids or readily digestible carbohydrates such as sugars, the activity of these bacteria is impaired, resulting in a reduction in the feed intake and digestion process. Different groups of microorganisms (mainly bacteria) are responsible for the digestion of starch-rich feed, such as grains. It has been reported that the activity of these microorganisms leads mainly to the production of propionic and lactic acids; therefore, if starch is provided excessively, their activity is accompanied by an increase in rumen fluid acidity and elimination of bacteria responsible for structural carbohydrate digestion. Unlike the above-mentioned bacteria responsible for structural carbohydrate digestion, these starch-digesting bacteria are rather insensitive to ruminal pH drop. The other form of sugar available in most diets is soluble sugars such as molasses and sugar cane. Similar bacteria are responsible for the fermentation of these sugars, as are for starch. Although fewer problems related to ruminal acidity are associated with soluble sugars, their gradual supplementation in the diet is advised. It has been mentioned by Moran (2005) that the digestibility of soluble carbohydrates is about 100- and 500-times faster than that of storage and structural carbohydrates, respectively.

In the end, some carbohydrates are converted to CO₂ and CH₄ during microbial fermentation. Methane is emitted through belching or absorbed by the rumen wall to some extent, while CO₂ can be partly metabolized by gastrointestinal microbes or utilized for maintaining bicarbonate levels in saliva (Moran 2005).

2.4 Protein digestion

Proteins that can be used by a ruminant, such as a dairy cow, can come from two sources: proteins in the fed diet and rumen microbes. When proteins are digested, they are broken down into their building units, polypeptides, peptides and amino acids, which can be further converted to ammonia (Chalmers et al. 1954). The microbial protein recovered by animals in the abomasum and intestine is dependent on the growth and washout of microbes from the rumen that further disintegrate down the digestion tract. On the other hand, there is the dietary protein available for the ruminant, which mainly includes the ingested rumen undegradable dietary proteins that have passed through the rumen without microbial conversion. These proteins are then digested together with the microbial proteins in the abomasum and intestine (Hvelplund 1984; Moran 2005). Most of the readily degradable proteins in the diet are broken down to amino acids and ammonia by rumen microbes, which further use ammonia as their main nitrogen source. The rumen microbes are also responsible for the production of ammonia from non-protein nitrogen. As discussed in Section 2.1, these microbes, which are the main source of protein for the ruminant, frequently flow from the rumen to the abomasum, where they are broken down, and then to the small intestine, where the resulting amino acids are absorbed by the walls. As presented by Moran (2005), the amount of microbial protein available to a cow is directly related to the energy and ammonia content of the feed. Simply put, the efficiency of ammonia uptake by rumen bacteria decreases as energy becomes scarce. The excess ammonia is then absorbed into the bloodstream, converted to urea in the liver and partly discarded through the urine or recycled as a non-protein nitrogen source through saliva. Similarly, diets with high carbon to nitrogen ratios, i.e. high in energy and low in protein, reduce microbial growth and therefore the microbial supply of protein to the ruminant. In lactating cows, a reduction in the total supply of protein results in a reduction in milk and milk protein yield.

2.5 Fat digestion

One of the other common feed components is lipids. Fat can be considered as a source of energy for the animal. Fat comprises only a small fraction of the dairy cow diet (less than 5% DM), as a surplus of dietary fat can interfere with fibre digestion and reduce diet palatability. A fraction of dietary fat is degradable by ruminal activity, and the fat escaping the rumen undigested is later digested and absorbed in the small intestine (Noble and Christie 1981). In general, protected fats (those that escape the undegraded rumen) are more favourable in the diet of lactating cows. For example, considering the dairy cows, protected fats from oilseeds are favourable, as they increase the energy content of the diet and help maintain energy during the lactation period (Moran 2005). The saturation level of the lipids provided in ruminant feed can also affect ruminal fermentation conditions. While a high content of polyunsaturated fatty acids (PUFAs) in feed may disturb the ruminal fermentation of fibres, saturated fatty acids (SFAs) are likely to have less effect on ruminal fermentation (Palmquist and Jenkins 1980; Havlin et al. 2015). This effect is associated mainly with the solubility of different fatty acids at normal rumen pH values (Schneider et al. 1988; Schauff and Clark 1989). As PUFAs may inhibit ruminal microbial activity, PUFAs are biohydrogenated as certain ruminal microbes add hydrogen atoms to the carbon-carbon double bonds, converting them to single bonds, thereby transforming unsaturated fatty acids to saturated fatty acids and reducing their toxicity, and along with that reducing the amount of PUFA absorbed by ruminants (Oldick and Firkins 2000; Freitas et al. 2018).

2.6 Ruminal fermentation of volatile fatty acids

In order to proceed with the effects of VFA supplementation on ruminants, understanding the basics of the natural fermentation of feedstuffs to VFAs and VFA metabolism in the rumen is necessary. VFAs, NH_4^+ , gases (CO_2 and CH_4) and lactic acid are the main end products of microbial fermentation in the rumen. The most common VFAs are acetate, propionate and butyrate. Rumen-generated VFAs that are absorbed through the rumen wall are transferred through the blood stream to the liver, mainly to be converted to different energy sources (Yao et al. 2017). Up to 80% of the metabolizable energy requirements of the animal are provided through VFAs, which can effectively be used for maintenance, growth and lipogenesis (Krehbiel 2014).

VFAs are derived mainly from dietary carbohydrates, but in the diet rich in the rumen, degradable protein and deaminated amino acids contribute to VFA generation through valine, leucine and isoleucine. Propionate is formed by the succinate pathway while both acetate and butyrate are formed from acetyl-CoA. The adenosine triphosphate (ATP) produced during fermentation is utilized by microorganisms for their maintenance and growth (Nozière et al. 2010). Depending on the diet (forage:concentrate ratio) and the rumen microbiota, the distribution of VFAs may vary and, for example, in lactating cows, can be a defining factor in the composition of milk constituents such as milk protein and fat. Forage-rich diets tend to increase the proportion of acetate, while concentrate-rich diets increase the proportion of propionate in the rumen fluid. Usually, 50%–70% of total ruminal VFAs are acetate, 15%–35% propionate and 10%–12% are butyrate, plus small amounts of other VFAs, such as isobutyrate and valerate. The balance between acetate and propionate (AcA:PrA ratio) is particularly important, as it influences both the efficiency of energy extraction from fermentation and how that energy is partitioned within the animal (Van Soest 2018). This ratio is also closely associated with methane formation (Ungerfeld 2020; Parchami et al. 2024). A higher A:P ratio is generally linked to increased methane output because greater acetate production releases more hydrogen, which methanogens use as a substrate in the hydrogenotrophic pathway. On the other hand, a decreased acetate-to-propionate ratio is typically associated with lower methane emissions, as propionate synthesis acts as a hydrogen sink. By utilizing hydrogen that would otherwise support methanogenic activity, propionate formation effectively limits methane production (Wang et al. 2018; Vargas et al. 2020).

VFAs are passively absorbed through the rumen wall, and this continuous removal of VFAs is very important for maintaining the ruminal pH. The absorption rate of VFAs is dependent on the chain length of the individual acids (butyrate > propionate > acetate) and the ruminal pH. Butyrate is, to a large extent, converted to ketones during absorption through the rumen epithelium. Butyrate is mainly converted to acetoacetate ($\text{C}_4\text{H}_6\text{O}_3$), as it is catabolized through the rumen epithelium (Kleiber et al. 1954). The mobilization of body fat can also generate ketones, which are used for the synthesis of fatty acids, production of body tissue and as energy sources. There is also the possibility for VFAs in the digesta to

flow and be absorbed in the omasum (Krehbiel 2014). Huntington (1990) reviewed that VFAs can be used to generate ATP in the intermediary metabolism. Unlike acetic and butyric acids, propionic acid can be used for the synthesis of glucose. As propionic acid is a precursor for glucose (providing 32%–73% of the cow's glucose demand), it is involved in the production of lactose (Aiello et al. 1989; Huntington 1990; Seal 1993). Propionate not only contributes to energy provision but also changes milk yield and composition. Accordingly, high-fibre diets in high-producing ruminants shift fermentation toward acetate at the expense of propionate, reducing the glucogenic energy supply. This energy deficit is then compensated by mobilizing body fat, which can lead to a loss of body condition.

3 Effects of volatile fatty acid addition to ruminant diet

This section provides an overview of the possible effects of dietary supplementation of three main VFAs on ruminants. Table 1 presents an extensive collection of literature regarding VFA supplementation in ruminant diets.

3.1 The effect of VFAs on gastrointestinal development

The development of the gastrointestinal tract of ruminants can be affected by VFA supplementation. Preliminarily, it was believed that the physical nature of the feed material is what stimulates rumen tissue growth, for example, in young ruminant forestomach. In this regard, since the late 1950s, the development of the rumen mucosa and papillary growth as an effect of supplementation with VFA salts such as NaAc, NaBu and NaPr has been the subject of different research works (Flatt et al. 1958; Sander et al. 1959). Flatt et al. (1958) reported the effectiveness of VFA salts and low-fibre purified diet on ruminal growth over coarse inert material (e.g. plastic sponge). The changes in rumen papillae size are one of the main development indicators in this regard.

Among rumen fermentation metabolites, butyrate is one that has proven to affect papillae and the epithelium. According to the literature, butyrate dietary supplementation enhances feed intake, growth (in calves), digesta retention and efficiency (in pigs), papillae size and the adsorption of ruminal metabolites (in goats and sheep) (Sander et al. 1959; Tamate et al. 1962; Gaebel et al. 1987; Vidyarthi and Kurar 2001; Shen et al. 2004; Clauss et al. 2009; Guilloreau et al. 2009; Le Gall et al. 2009). Moolchand et al. (2013) observed that when a group of goats were fed with excess amounts (0.3 g per kg body weight (BW) per day) of NaBu in addition to the basal diet of concentrate and hay, the height of papillae, epithelium thickness, ruminal VFA concentration, rumen digesta weight and empty rumen weight increased compared to the control group fed the basal diet only. However, this supplementation did not affect the ruminal fluid outflow and resulted in a reduction in omasum weight. In addition to promoting rumen papillae development, butyrate supplementation to newborn calves in the form of NaBu, separately or together with a milk replacer (MR), has been proven to have prebiotic effects (Górka et al. 2014; Ragionieri et al. 2016; Górka et al. 2011a, 2011b). In addition, Gorka et al. (2009) showed that feeding bull calves with 3 g/kg DM NaBu together with MR for 21 days resulted in reticulorumen weight gain, rumen papillary growth and animal weight gain. In another study by Kowalski et al. (2015), as expected, by supplementation of microencapsulated NaBu together with the basal total mixed ration (TMR), factors related to rumen papillae development, such as length, cross-sectional surface area and rumen muscle layer thickness, increased in bulls. On the other hand, for lactating cows, the postpartum rumen diet adaptation period was enhanced when NaBu was fed together with TMR. However, apart from the site of VFA salt administration, the form in which it is introduced to the animal is also highly important. When NaBu is added to a starter mixture in the form of NaBu encapsulated in a triglyceride matrix, it stimulates rumen development directly, while an indirect positive effect is expected when added as NaBu crystals to milk replacer in the treatment of newborn calves (Górka et al. 2011a).

Supplementation of NaPr and NaAc in a sheep diet has also been reported to yield rather similar effects as NaBu (Sakata and Tamate 1979). Moreover, Sander et al. (1959) claimed that the supplementation of NaBu and NaPr has a more profound effect on rumen papillae development in young dairy calves compared to NaAc, glucose or NaCl. In the aforementioned research, the effects of NaBu and NaPr on blood flow in the rumen and the metabolism of specific compounds by the rumen wall were considered.

Table 1. Studies on dietary supplementation of VFAs in ruminants' feeds. The literature is listed in chronological order.

Supplemented VFAs	Supplied amount	VFAs blend (wt%)	VFA administration method	Subject ruminants	# Subjected ruminants	Experiment period (days)	Ref.
NaBu	2% of DM	100% NaBu	Added to diet DM	Lactating cows	8	21	Fukumori et al. (2020)
PrA	4 ml or 4 g/kg natural matter	100% PrA	Added to diet DM	Lactating cows	25	19	Gheller et al. (2020)
NaAc	2.87% of DM	100% NaAc	Added to diet DM	lactating cows	12	14	Urrutia et al. (2019)
CaBu	2.47% of DM	100% CaBu	Added to diet DM	Lactating cows	8	21	Izumi et al. (2019)
NaBu	2% of DM	100% NaBu	Added to diet DM	Lactating cows	8	21	Izumi et al. (2019)
CaPr	30–40 g/kg of DM	100% CaPr	Added to diet DM	lambs	32	42	Cifuentes-lópez et al. (2018)
NaBu	1–2 g/kg BW day	100% NaBu	Ruminal and abomasal infusion	Lactating cows	5	3	Herrick et al. (2018)
CaPr	200 g/day	100% CaPr	Added to diet DM	Finishing bulls	8	51	Yao et al. (2017)
NaBu	1–2 g/kg BW day	100% NaBu	Ruminal infusion	Lactating cows	4	3	Herrick et al. (2017)
Lac	3.5 g/kg BW day	-	-	-	-	-	-
CaPr	50–100 g/kg DM	100% CaPr	Added to diet DM	Calves	54	160	Zhang et al. (2017)
NaPr	240 g/day	100% NaPr	Oral supplementation	Lactating cows	84	14	Dorn et al. (2016)
CaBu	5 g/day	100% CaBu	Added to diet DM	Bulls	85	118	Moreira et al. (2016)
CaPr	10 g/day	100% CaPr	Added to diet DM	lambs	21	42	Mendoza-Martínez et al. (2016)
NaBu	90 g/day	100% NaBu	Added to diet DM	lactating cows	26	90	Kowalski et al. (2015)
	0.6% of DM			Bulls	12	21	
NaPr	5% of DM	100% NaPr	Added to diet DM	Calves	42	70	Beiranvand et al. (2014)
NaBu	0.3 g/kg BW day	100% NaBu	Ruminal infusion	Goats	15	28	Moolchand and Wang (2013)
CaPr	0–10 g/kg of DM	100% CaPr	Added to diet DM	Lambs	32	40	Lee-Rangel et al. (2012)
Pr	800 g/day	100% Pr	Ruminal infusion	Lactating cows	6	21	Maxin et al. (2011a)
Ac	1500 g/day	100% Ac					
Pr + Ac	400 g/day	34.8% Pr, 65.2% Ac					
CLA	750 g/day	100% CLA					
CLA + Pr	1.6 g/day	0.2% CLA, 99.8% Pr					
NaBu	1.6 g/day + 800 g/day						
	3 g/kg of DM	100% NaBu	Oral supplementation/ added to the diet	Calves	28	21	Górka et al. (2011a)
NaPr	150 g/day	100% NaPr	Added to diet DM	Steers	8	42	Sparks et al. (2011)
AcA	132 g/kg BW	100% AcA	Ruminal infusion	Sheep	24	12	Ma and Zhao (2010)
PrA	0.75 day	100% PrA					
BuA		100% BuA					
VFA mixture		10% AcA, 78% PrA, 12% BuA					
		27% AcA, 65% PrA, 8% BuA					
		49% AcA, 47% PrA, 4% BuA					
		60% AcA, 38% PrA, 2% BuA					
NaBu	3 g/kg of DM	100% NaBu	Oral supplementation or duodenal infusion	Calves	8	34	Guilloteau et al. (2010)
CaPr	100–300 g/day	100% CaPr	Added to diet DM	Steers	8	21	Liu et al. (2009)
NaBu	3 g/kg of DM	100% NaBu	Oral supplementation	Calves	88	154	Guilloteau et al. (2009)
NaBu	3 g/kg of DM	100% NaBu	Oral supplementation	Calves	14	21	Gorka et al. (2009)
BuA	500 g/day	100% BuA	Ruminal infusion	Bulls	3	14	Shen et al. (2005)
PrA	13 mol/day	100% PrA	Ruminal infusion	Lactating cows	5	14	Rigout et al. (2003)
PrA + VFA mixture	7.3 mol/day + 6.5 mol/day	PrA + (53.9% AcA, 20.4% PrA, 25.6% BuA)					

(Continued)

Table 1. (Continued)

Supplemented VFAs	Supplied amount	VFAs blend (wt%)	VFA administration method	Subject ruminants	# Subjected ruminants	Experiment period (days)	Ref.
AcA	300 kcal/day	100% AcA	Ruminal infusion	Sheep	4	12	Fujihara et al. (2002)
PrA	300 kcal/day	100% PrA					
BuA	150 kcal/day	100% BuA					
BuA	12–24 ml/day	100% BuA	Added to milk	Calves	18	120	Vidyarthi and Kurar (2001)
NaBu and KBu	54.4–326.4 g/day	50% NaBu, 50% KBu	Oral supplementation	Calves	9	42	Mentschel et al. (2001)
NaPr and KPr	52.8–390.9 g/day	50% NaPr, 50% KPr					
NaPr	5% of DM	100% NaPr	Added to diet DM	Lambs	12	12	Berthelot et al. (2000)
NaPr	0–40 g/kg of DM	100% NaPr	Added to diet DM	Wethers	24	28	Moloney (1998)
PrA	13.4 mol/day	100% PrA	Ruminal infusion	Lactating cows	4	14	Hurtaud et al. (1998)
VFA mixture	17 mol/day	64% AcA, 21% PrA, 15% BuA)					
PrA	0–900 g/day	100% PrA	Ruminal infusion	Lactating cows	4	14	Miettinen and Huhtanen (1996)
BuA	0–750 g/day	100% BuA					
PrA + BuA		67% PrA, 33% BuA (energy basis)					
VFA mixture	450–900 kJ/kg BW day	45% AcA, 45% PrA, 10% BuA	Ruminal infusion	Sheep	36	7–14	Orskov et al. (1979)
		55% AcA, 35% PrA, 10% BuA					
		65% AcA, 25% PrA, 10% BuA					
		75% AcA, 15% PrA, 10% BuA					
		35% AcA, 55% PrA, 10% BuA					
		85% AcA, 5% PrA, 10% BuA					
NH ₄ Ac	252–1252 g/day	100% NH ₄ CH ₃ CO ₂	Oral supplementation	Lactating cows	12	21	Webb et al. (1973)
AcA + PrA	3%–9% of DM	70% AcA, 30% PrA	Added to diet DM	Lactating cows	50	84	Jones (1971)
		50% AcA, 50% PrA			10	21	
		30% AcA, 70% PrA		Sheep			
AcA	500–1000 ml/day	100% AcA	Ruminal infusion	Lactating cows	6	42	Wilson et al. (1967)
PrA		100% PrA					
BuA	370–738 ml/day	100% BuA					
NaAc and CaAc	20% of DM	50% NaAc, 50% CaAc	Added to diet DM	Lambs	40	73–122	Ørskov and Allen (1966)
NaBu and CaBu	–						
NaPr and CaPr	–	50% NaBu, 50% CaBu					
		50% NaPr, 50% CaPr					
AcA	100–400 Cal./every other day	100% AcA	Ruminal infusion	Sheep	2	7	Ulyatt (1965)
PrA		100% PrA					
Bu	-	100% Bu	Intravenous injection	Lactating cows	6	–	Black et al. (1961)
NaAc	200–239 g/day	100% NaAc	Ruminal infusion	Calves	12	77	Martin et al. (1959)
NaBu		100% NaBu					
NaPr		100% NaPr					
NaBu	4.4–9.7 mM	100% NaBu	Intravenous injection	Lactating cows	4	–	Kleiber et al. (1954)

Note: acetate (Ac), acetic acid (AcA), sodium acetate (NaAc), calcium acetate (CaAc), ammonium acetate (NH₄Ac), butyrate (Bu), butyric acid (BuA), calcium butyrate (CaBu), potassium butyrate (KBu), propionate (Pr), propionic acid (PrA), sodium propionate (NaPr), calcium propionate (CaPr), potassium propionate (KPr), conjugated linoleic acid (CLA) and lactose (Lac).

However, the next question to be answered is the superiority of butyrate over propionate or vice versa in the promotion of ruminal papillary growth and the mechanism behind this growth promotion. This has been clarified to an extent in a study by Mentschel et al. (2001). Their obtained results showed that the length of the rumen papillae had increased 2.2- and 4-times in the calves fed with propionate and butyrate, respectively, compared to calves fed a basal diet of hay grass and MR only. The apparent increase in the mitotic rate during VFA supplementation was presented as the reason for this difference in papillae size compared to the control. Furthermore, the ruminal apoptotic rate was as low as one-third when calves

received butyric acid compared to propionic acid. On the other hand, butyrate supplementation enhanced papillary growth more than what was recorded for propionate (Mentschel et al. 2001).

3.2 The effect of VFAs supplementation on milk yield and composition

A complex molecular mechanism is responsible for the synthesis of different fractions of milk, such as fat and protein, in mammary glands during lactation (Haug et al. 2007; Mcmanaman 2009). Although diverse and sometimes contradictory outcomes have been presented in different studies, Wilson et al. (1967) reported that all three main fatty acids increase milk yield. Among milk constituents, the fat content of milk is considered the most sensitive to the content and composition of nutrients in the diet (Harvatine et al. 2009). In general, a relative increase in the milk fat content is associated with the infusion of VFAs such as acetate and butyrate (Maxin et al. 2011b; Urrutia and Harvatine 2017b). In the mammary glands of dairy cows, milk fat production is stimulated by an increase in the predominant precursors of *de novo* synthesis of FAs, beta-hydroxybutyrate (BHB) and acetate levels (Bauman et al. 1970; Smith et al. 1974; Zhang et al. 2015a; Urrutia and Harvatine 2017b). Changes in gene expression induced by BHB and acetate in bovine mammary epithelial cells were thoroughly discussed by Song et al. (2020). Although the findings in different studies may appear contradictory in certain instances, a collection of conclusions made regarding the effects of VFA supplementation on milk yield and composition are presented here.

Diverse results have been reported upon the supplementation of butyrate salts or butyric acid to lactating cows. Izumi et al. (2019) found that the inclusion of butyrate in the form of NaBu (2% DM) not only increases milk fat yield and content but also reduces the milk urea nitrogen (MUN) without affecting dry matter intake (DMI) or increasing the risk of subclinical ketosis. However, Kowalski et al. (2015) reported that the DMI, BHB, nonesterified fatty acid (NEFA), rumen pH, ruminal VFA ratio, $\text{NH}_3\text{-N}$ concentration and milk yield were not noticeably affected by NaBu supplementation in bulls and lactating cows. On the other hand, supplementation of the basal diet with 2.9% and 2.5% (percentage of DM) of NaAc and CaBu (the carbon equivalent based on acetate was considered), respectively, did not affect the milk yield in the treatments receiving NaAc, while the ones with CaBu reduced the milk yield by 1.65 kg/day (Urrutia et al. 2019). In addition, it has been reported that butyrate can also play a role in lactose synthesis, while acetate mainly contributes to milk fat synthesis. In lactating cows, butyrate mainly contributes to carbohydrate synthesis (glyconeogenic) rather than being lipogenic while for acetate, the opposite applies (Kleiber et al. 1954). In contrast, in a later study Bhatia et al. (1978) disapproved this claim, as they have traced and detected butyrate in both milk lactose and fat.

The ratio between VFAs in the infused supplement can also alternate features such as milk yield and blood metabolites in lactating cows. For example, when Miettinen and Huhtanen (1996) conducted an isoenergetic experiment where dairy cows were provided with ruminal infusion of varying ratios of PrA:BuA between 1:0 (900 g/day PrA and no BuA) and 0:1 (750 g/day BuA and no PrA), as the PrA:BuA ratio decreased, so did the milk yield, lactose production and plasma glucose levels. However, replacement of BuA with PrA in the infused supplement resulted in a metabolic shift, leading to an increase in the production of long-chain fatty acids (LCFAs), blood ketone body, acetate and branched-chain amino acid (BCAA) contents in the plasma. Although, conformingly, when butyrate dietary infusion was increased by Huhtanen et al. (1993), milk lactose and plasma glucose concentrations dropped while the milk yield was not affected. This is justified by the fact that the cows subjected to the above-mentioned research already benefitted from a positive energy balance that was not disturbed by a decrease in the plasma glucose content. Moreover, it should be considered that as the butyrate supplementation increases, propionate and acetate provision is downregulated; therefore, the results acquired include a combined effect (Huhtanen et al. 1993; Miettinen and Huhtanen 1996).

In the milk and dairy industry, milk fat is of great importance and market value, as it defines the final characteristics and properties of dairy products. In this context, efforts have been made to explore dietary approaches to manipulate milk fat synthesis. There are two pathways that supply milk FAs: FAs resulting from *de novo* synthesis in the mammary gland and FAs provided from plasma FA uptake (absorption from the diet or endogenous reserves) (Urrutia et al. 2019). The supplementation of VFAs such as acetic acid plays an important role in the *de novo* synthesis of FAs. Among the main VFAs produced through ruminal fermentation, acetate is the main energy contributor (energy from VFA metabolism) and the predominant

precursor for *de novo* synthesis of FAs (Urrutia et al. 2019). As an example, acetate can act as 2-carbon donor for malonyl-CoA synthesis (Bauman et al. 1970; Ingle et al. 1973; Smith 1983). Malonyl-CoA is the precursor that primarily provides the required carbon source for fatty acid chain elongation by the enzyme fatty acid synthase (FASN) (Lalotiotis et al. 2010).

As presented by Urrutia and Harvatine (2017b), most of the research revolving around the effect of acetate supplementation on milk fat synthesis was focused on the years between 1955 and 1978. Having in mind that recent research and experimentation strategies are notably different from those used prior to the 1980s (generally involved very limited animal replication, used low-producing cows and were based on diets that differ considerably from modern rations), their results concluded that milk fat (both yield and concentration) increases relative to the increase in the diet acetate infusion (Maxin et al. 2011b). These findings were further supported (Urrutia and Harvatine 2017a), as linear and quadratic increase in milk fat concentration and yield, respectively, was recorded when lactating cows received a ruminal infusion of acetate (pH 6.0). On the other hand, acetate infusion has been reported to contribute to an increase in plasma BHB by conversion to butyrate in the rumen or rumen wall (Sutton et al. 2003). This increase in BHB levels caused by acetate infusion becomes of remarkable interest when considering that BHB is a main carbon contributor for the *de novo* synthesis of FAs (Palmquist et al. 1969).

Urrutia et al. (2019) studied milk fat synthesis in lactating cows fed with acetate and butyrate and reported that, while a diet of 2.9% (DM-based) NaAc led to a 90 g/day increase in milk fat, provision of 2.5% CaBu caused a 60 g decrease in daily fat production. Such contradictory effect of VFAs was reported for the changes in the dry matter intake by the cows. Considering the effects of supplementation with acetate and butyrate on 16 carbon mixed source FA concentrations in milk, while an increase in yield and concentration was reported for NaAc, CaBu supplementation did not lead to any noticeable changes in milk FA concentration. However, CaBu caused alternations in the rumen biohydrogenation pathway, resulting in an increase in *trans*-10 C18:1 (Urrutia et al. 2019).

To investigate the effect of propionate on milk fat yield and composition, Rigout et al. (2003) infused PrA or glucose in the rumen and duodenal of lactating cows while sustaining isoenergetic and isonitrogenous treatments. They observed that, in both treatments, the milk yield and protein yield increased, followed by a decrease in DMI, in the VFA infusion treatment group compared to control treatment, while in confirmation with other studies, extragluconic precursor (GP) supplementation resulted in a decrease in milk fat yield. The reported increase in the milk yield compared to the control group indicates that the poor supply of GP in a grass silage-based diet has been compensated by the supplementation of PrA and glucose. The main difference between the treatments that received glucose and PrA lied in the final fatty acid composition of the milk fat. A decrease in milk fat together with an increase in protein yield in lactating cows intraruminally supplemented with propionic acid has also been confirmed by Hurtaud et al. (1998).

It has become common knowledge that feed containing high portions of concentrate and low portions of forage yields less milk fat in lactating cows. Although a milk fat depression (MFD) diet (typically high-concentrate and low-forage rations) can cause up to 50% drop in the milk fat, amount of milk and other milk constituents may undergo negligible changes. One reason for this fat depression is discussed through the biohydrogenation theory. Feeding a dairy cow with a MFD diet changes lipid metabolism in the rumen, resulting in the formation of lipid synthesis inhibitory compounds such as *trans* fatty acids and conjugated fatty acid (CFA) such as *trans*-10, *cis*-12-conjugated linoleic acid (CLA) (Maxin et al. 2011a). However, this theory can be challenged considering the insufficiently low rumen outflow of these compounds (Bauman and Griinari 2001, 2003; Roy et al. 2006; Shingfield and Griinari 2007; Harvatine et al. 2009; Shingfield et al. 2010). Moreover, a decrease in ruminal pH in diets rich in concentrates induces a metabolic shift favouring propionate production (Bauman et al. 1971; Sutton et al. 2003). This rise in ruminal propionate levels, as also reported in the case of ruminal infusion of propionate, results in the presence of odd-chain FAs in milk (Hurtaud et al. 1998; Rigout et al. 2003; Maxin et al. 2010; Maxin et al. 2011a). In this context, Maxin et al. (2011a) found that the addition of propionate and CLA resulted in 9% and 15% reductions in milk fat yield and content, respectively. The inhibitory effect of propionate became more pronounced when the propionate was added together with CLA. Co-supplementation of propionate and CLA resulted in a 40% more milk fat reduction compared to a treatment involving only similar dose of CLA.

3.3 The effect of VFAs supplementation on dry matter intake and weight gain

Dry matter intake—regardless of the site of introduction (e.g. intraruminal infusion or addition to the feed ration), VFA supplementation may have different effects on feed consumption. Although ruminal infusion of VFAs has been reported to have an inconsiderable effect on the eating time and rumination behaviour of sheep (Fujihara et al. 2002), it has been associated with the depression of feed intake in ruminants. This may be considered as one of the reasons behind the irrational changes in milk yield and composition in lactating cows (Baile and Mclaughlin 1970; Jones 1971). However, the consistency of findings regarding the effects of VFAs on DMI is a matter of question.

When about 252–1252 g/day acetate was fed to lactating cows in the form of ammonium acetate alongside cane molasses, no changes in feed intake were observed by Webb et al. (1973). In contrast, an earlier study by Ulyatt (1965) reported that the effect of AcA on DMI depression is more pronounced than that of PrA and BuA. As claimed, while 200 calories of AcA supplementation to sheep can result in significant feed intake depression, such a change is observed when PrA and BuA supplementation are as high as 300 and 400 calories, respectively (Ulyatt 1965).

Live weight gain—VFAs are fed through the diet in the form of solid VFA salts or infused as supplements. It has been reported that young sheep can have normal weight gain over considerably long periods with a diet of rumen-infused VFAs and abomasal-infused protein (Orskov et al. 1978). In this context, Ørskov and Allen (1966) reported that if the treatment is isoenergetic using different Na or Ca salts of acetate, propionate and butyrate will result in rather similar live weight gain outcomes.

In general, the effect of VFA salt supplementation on ruminant weight gain is rather controversial. It has been recorded that intraruminal supplementation of VFA salts enhances the early stage development of rumen and consequently enhances weight gain (Hibbs et al. 1956; Vidyarthi and Kurar 2001). However, these findings cannot be generalized as, for instance, in calves, the surplus provision of dietary VFA salts, sponges or a purified diet plus milk has caused an increase, a reduction or no noticeable change in total body weight gain when compared to an only milk diet (Flatt et al. 1958; Martin et al. 1959; Morrill et al. 1981; Anderson et al. 1982, 1988). When Vidyarthi and Kurar (2001) compared buffalo calves fed only with a basal diet with those receiving additional butyric acid (12–24 ml/day), they recorded higher body weight gain and digestibility of diet components (DM, crude protein (CP), organic matter (OM), neutral detergent fibre (NDF), acid detergent fibre (ADF), ether extract, cellulose and hemicellulose) for the latter treatments, with the optimum addition being 24 ml/day. Although this is in conformation with findings of Anderson et al. (1988), Hibbs et al. (1956) and Morrill et al. (1981), these results are opposed in a number of other literature published during the same time interval (Flatt et al. 1958; Martin et al. 1959; Singh et al. 1973).

Since 1950's different antimicrobial compounds have been used to promote animal weight gain and growth while providing a cost efficient process (Visek 1978; Hardy 2002). However, the human and animal health concerns on issues regarding antimicrobial resistance resulted in the European Union ban on the application of such substances in animal diet from 2006. This was one of the incentives to investigate the effect of the application of VFAs for ruminant growth improvement as a replacement for antimicrobial compounds. In a study, Guilloteau (2009) compared the effects of the addition of the growth-promoting antimicrobial compound, flavomycin and NaBu on the development of the gastrointestinal tract (digestive enzyme activity, defence system, plasma gut regulatory peptide concentrations, etc.) and the growth of milk-fed calves. It was found that calves supplied with 3 g of NaBu per kg of DM instead of flavomycin experienced higher growth rate and feed-to-body weight conversion. This may root in the effects attributed to butyrate in improving digestive capacities.

3.4 The effect of VFAs supplementation on hormones

The effects of VFAs on hormone types and concentrations in ruminants have long been a topic of research interest. In this context, changes in hormones such as insulin, glucagon, insulin-like growth factor-I (IGF-I), glucagon-like peptide-2 (GLP-2) etc. based on factors, such as type, concentration and ratio of supplemented VFAs, and site and frequency of administration, have been studied.

The links between the presence of hormones, e.g. insulin, IGF-I and epidermal growth factor and VFAs with rumen development have been the focus of different *in vivo* and *in vitro* studies (Sakata et al. 1980;

Neogrady et al. 1989; Baldwin 1999; Baldwin et al. 2004). Considering the role of IGF-I in growth regulation (Cohick and Clemmons 1993), it is important to understand the role that VFAs play in the secretion of IGF-I. According to Zhao and Sun (2010), IGF-I levels in plasma and tissues increased as the level of ruminally infused mixed VFAs was increased. However, as they investigated the effects of AcA, PrA and BuA individually or as a mixture with different molar portions in isoenergetic treatments on solely intragastrically fed sheep, it was observed that plasma and tissue IGF-I levels and papillae growth did not alter considerably (Ma and Zhao 2010). The outcome is further justified by the isoenergetic nature of the treatments (Ma and Zhao 2010). However, when Shen et al. (2005) intraruminally infused bulls with BuA, although an increase in rumen papilla length, width and surface area (20%–40% increase in surface area compared to control group) was observed, this led to a reduction in plasma IGF-I levels. It can be concluded based on the above-mentioned findings that BuA supplementation interferes with the regulation of papilla growth by IGF-I and IGF type I receptors.

Butyrate can also contribute to other gastrointestinal functions by changing the concentration of GLP-2 that stimulates and regulates intestinal tissue growth (Gorka et al. 2009; Fukumori et al. 2020). The secretion of GLP-2 by the intestinal epithelial cells can result increase in epithelial proliferation, inhibition of apoptosis, and enhancement of barrier function, digestion, absorption and blood flow (Markovic and Brubaker 2019). When Fukumori et al. (2020) tracked the changes in the plasma GLP-2 concentrations in two groups of dairy cows, one with a high starch diet (27.5% starch) and the other with a low starch diet (20.6% starch) both supplemented with NaBu, they recorded higher plasma GLP-2 levels for the former treatment. In both cases, the dietary supplementation of NaBu (2% of DM) increased total tract digestibility. These changes in hormone levels (insulin and growth hormone) were also observed by Fuhrmann et al. (1989) when heifers and cows received an overload of butyrate and propionate along with glucose through intravenous infusions.

Due to ruminal fermentation, only a small amount of dietary carbohydrates remains as hexose sugars (Phillipson 1970; Bergman 1973), and gluconeogenesis (synthesis of glucose from non-carbohydrate sources) is the main process for providing ruminants with the required glucose (Ballard et al. 1969). In ruminants, propionate, lactate/pyruvate, amino acids and glycerol play the main role as glucogenic substrates (Baile et al. 1969). The energy metabolism and blood sugar levels in ruminants are tightly regulated by the opposing actions of insulin and glucagon, as reviewed in different studies (Bassett 1975; Brockman 1978). The peripheral, muscle and adipose tissues are the target action sites for insulin, where this hormone facilitates the uptake and utilization of glucose. However, in ruminants, this process is less insulin-dependent (Peters et al. 1983). Insulin secretion in ruminants is stimulated more by intravascular infusion of propionate, valerate and butyrate than by glucose (Manns and Boda 1967a). Additionally, glucagon secretion can be elevated by administering butyrate and propionate (Argenzio 1981; Bergman 1990). In various studies, the role of VFAs as a humoral factor and as a stimulant for endocrine pancreatic secretion in sheep (Nord et al. 1983), cow (Horino et al. 1968) and goat (Bergman, 1990) has been mentioned. Horino et al. (1968) investigated the effect of infused 3–8 carbon atoms of fatty acids on blood content. They reported a 4-fold increase in insulin level for propionate and a 14-fold for butyrate. Husveth et al. (1996) have also reported significant elevation in blood glucose levels by propionate and n-valerate infusion. However, butyrate infusion did not boost glucose increase as for propionate and valerate. The indication of earlier results proposes that a pronounced hyperglycemic effect is caused by VFAs with a glucogenic nature, such as propionate and valerate (Bergman et al. 1966; McAtee et al. 1971), though, VFAs with ketogenic features, such as butyrate enforces a mild impact on the glucose level, while no effect was observed by acetate infusion (Jones et al. 1970; Manns et al. 1967b).

The carbon number and the form of hydrocarbon (branched or straight) in VFAs influence the hormone secretory activity of the pancreas. In other words, the chemical structure of VFAs directly influences pancreas hormone-secreting cells. Mineo et al. (1994) found that n-butyric acid and n-valeric acid were the most effective VFAs for insulin secretion; in contrast, formic acid had no effect. Besides, the VFAs with six carbon atoms have great potential for stimulating insulin generation (Ambo and Hideyuki 1973). However, the effect of acetate is not well defined. Trenkle (1972) reported acetate's moderate effect on insulin generation, while Manns and Boda (1967a) reported no effect. The carbon chain length as an inducer of glucagon and insulin responses, is slightly diverse. Three to seven carbon atoms are claimed by Brockman (1978) to be the proper stimulators for insulin secretion while VFAs of two to six carbon atoms also induce glucagon.

Feeding frequency and diet type would alter the VFA molar ratio in the rumen, which ultimately affects insulin and glucagon plasma concentrations (Sutton et al. 1988; Sano et al. 1995). Ostaszewski and Barej (1979) utilized two different rations (ration one composed of sugar beet silage, a urea-mineral preparation, meadow hay, and ration two composed of soybean meal, dried sugar beet pulp and meadow hay) in order to determine the relationships between VFAs and insulin and glucagon levels. Ration one resulted in more butyrate, propionate and acetate generation, which led to elevated insulin and blood glucagon levels. This could possibly be the effect of the increase in blood flow through the pancreas, as this increase is one of the prerequisites for increase in pancreatic hormone release. Factors such as intensification of rumen fermentation and the elevation in VFA production can increase blood flow to visceral organs (Leontowicz et al. 1979).

After the infusion of propionate and valerate, a rapid glucose synthesis occurs in the liver. This process generates glucose in the peripheral circulation, increasing the blood glucose concentration (Gross et al. 1990). In this context, Husveth et al. (1996) have claimed that valerate has higher glucogenesis-enhancing potential than propionate and butyrate. In addition, butyrate is reported to directly enhance the hepatic glycogenolysis through an increase in glucagon secretion, resulting in blood hyperglycaemia (Jones et al. 1970). This hypothesis was backed by De Jong (1982), who reported higher stimulatory effect on glucagon secretion by butyrate than propionate and valerate.

The site of infusion of VFAs can also define metabolite concentrations in the blood. Ruminal and abomasal infusion of 1–2 g/kg BW of NaBu to lactating cows showed that while in both cases, plasma BHB increased, plasma glucose decreased for ruminal infusion but not for abomasal infusion (Herrick et al. 2018). The infusion of supplementary butyrate did not change the plasma insulin levels in either of the treatments in this study by Herrick et al. (2018). However, the intravenous and intraruminal administration of butyrate may lead to rather diverse effects. While intraruminal supplementation of butyrate of more than 10 mmol/kg BW to ruminants such as sheep, goats and lactating dairy cows is claimed to induce hypoglycaemia and hyperketonaemia, supplementation of less than one-fourth of it to insulin-treated lambs, sheep and lactating dairy cows and goats can lead to a glucose surge in the blood (Hamada et al. 1984). Oral supplementation or duodenal infusion of dietary NaBu has also been claimed to result in different metabolic and physiologic effects in young calves (Guilloteau et al. 2010). The calves orally fed with NaBu (3 g/kg of DM) in addition to the basal milk formula enjoyed an improvement in nutrient digestibility and daily pancreatic secretions. In contrast, except a rise in lipase levels, duodenal infusion of NaBu did not affect pancreatic secretions.

In general, the stimulatory effects of VFAs on the secretory action of the pancreas are diverse. Although VFAs with higher carbon atoms might have a premier influence, other factors, such as ration type, amount of VFA infusion and feeding frequency, also contribute to the observed effects.

3.5 The effect of VFAs supplementation on rumen microbiota

In order to be able to break down dietary material (mainly plant-based feedstuff) to extract maximal energy and nutrients, ruminants benefit from an army of ruminal microorganisms. Considering that VFAs are natural metabolites generated from ruminal fermentation, their *ex-situ* supplementation can induce alternations in the ruminal microbiota.

Considering the nutritional importance of propionate for ruminants and the effects of supplementation with propionic acid and propionate salts on changes in milk composition and constituent levels, protein yield, DM intake and digestibility, carcass index and more (Miettinen and Huhtanen 1996; Hurtaud et al. 1998; Moloney 1998; Rigout et al. 2003; Mcnamara and Valdez 2005; Liu 2009; Sanchez et al. 2014; Lee-Rangel et al. 2012), some examples of changes in the ruminal microbiota caused by propionate supplementation are presented here. The effects of propionate supplementation in steers on functional and phylogenetic changes in the rumen microbiota have been studied through metagenomics characterization by Sparks (2011). Spark (2011) reported a reduction in the abundance of *Fibrobacter succinogenes* when propionate was administered exogenously to steers. Unlike Gram-negative bacteria, Gram-positive bacteria are reported to thrive by propionate supplementation, resulting in the respective domination of *Bacteroidetes*, *Firmicutes* and *Proteobacteria* in the rumen. Regarding the effect of calcium propionate (CaPr) supplementation on the composition of the rumen microbiota, Yao et al. (2017) found that the bulls

fed with the basal TMR and TMR plus 200 g/day additional CaPr ended up having rather similar rumen bacterial compositions and subsequently similar fermentation parameters. Although for both reported study groups of bulls, *Firmicutes*, *Bacteroidetes*, *Tenericutes* and *Saccharibacteria* (TM7) were the most abundant ruminal phyla, the group supplemented with CaPr experienced a reduction in the abundance of *Tenericutes*.

3.6 The effect of VFAs on adipose tissue

Adipose tissue metabolism in ruminants has been studied because of its importance in animal production and differences in fatty acid synthesis between ruminants and non-ruminants. The leading site for the synthesis of fatty acids in a non-lactating ruminant is adipose tissue. In this context, VFAs play the role of precursors for fatty acid synthesis. This has been revealed by *in vivo* tracking of the metabolism of acetate in ruminants (Hanson and Ballard 1967; Ingle et al. 1972). The *in vivo* studies by Ingle et al. (1973) revealed that, in non-lactating sheep, more than 90% of fatty acids are synthesized by adipose tissue. An earlier study showed that acetate, rather than glucose, is the primary precursor for fatty acid synthesis in ruminant mammary glands (Mills and Jenny 1979). Following that, a number of studies confirmed the role of acetate as the main precursor for fatty acid synthesis in both perirenal and subcutaneous adipose tissue of sheep, cattle and goats (Vernon 1976; Whitehurst et al. 1978; Vernon 1981). One reason for this could be the faster incorporation of acetate carbon into fatty acids (10–100 times more rapid) than glucose carbon; hence, acetate carbon has an outstanding role in providing C2 units for fatty acid synthesis (Chakrabarty and Romans 1972). Robertson et al. (1981) determined the contribution rate of acetate, L-lactate and glucose to fatty acid synthesis in adult sheep adipose tissue. According to this study, acetate is a preferable precursor compared to glucose and L-lactate, accounting for about 95% of the C2 units required for fatty acid synthesis, while its elimination from the incubation medium leads to a considerable reduction in the total rate of fatty acid synthesis. In addition, they found that the acetate contribution rate tended to decrease in the adipose tissue of foetal lambs about 30 days prior to birth compare to adult sheep, as acetate provided 50% of the C2 units for fatty acid synthesis, whilst L-lactate and glucose provided 33 and 17%, respectively (Chakrabarty and Romans 1972).

Regarding the type of fatty acids generated, acetate has been referred to as the main precursor for the synthesis of palmitic, stearic and oleic acids in bovine and ovine adipose tissue. However, the age of the animal, type of ration and concentration of acetate diversify the amount of synthesized fatty acids in adipose tissue.

The site of fatty acid formation is different; abdominal adipose tissue favours stearic acid synthesis while subcutaneous adipose tissue favours oleic acid synthesis (Pothoven et al. 1974). There are odd-numbered and methyl-branched fatty acids in various subcutaneous adipose tissues that are in part accountable for the usually smooth subcutaneous fat. These fatty acids provoke a lower melting point and cause a lack of firmness in the carcass. One reason for this can be the overflow of propionate resulting from ruminal fermentation of easily fermentable carbohydrates in the animal's diet to the liver. The unmetabolized propionate in the liver could be used as a substrate in dorsal and perirenal adipose tissue for the synthesis of the above-mentioned fatty acids (Garton et al. 1972). Berthelot et al. (2000) findings confirmed the role of propionate as a precursor for fatty acid production. They added NaPr to a carbohydrate-rich diet and evaluated the proportion of fatty acids in three adipose tissue sites (dorsal, caudal and sternal). A significant increase in the composition of odd-numbered fatty acids was recorded at all three sites from animals fed with propionate. In addition, there was a tendency in dorsal adipose tissue for an increase in methyl branched fatty acids.

As mentioned in the previous sections, CaBu acts as a growth-promoting agent. The supplementation of CaBu and *Bacillus subtilis* (probiotic performance enhancer) in bull rations has been reported to increase the subcutaneous fat thickness (Moreira et al. 2016).

3.7 The effect of VFAs on meat quality and intramuscular fat

The deposition of intermuscular fat in ruminant carcass is considered unpleasant, whereas a noticeable amount of intramuscular fat positively affects the palatability specifications of the meat, known as the

marbling characteristic (Blumer 1963). This attribute is welcomed by meat consumers because of its positive impact on the tenderness, flavour and juiciness of the meat (Wang et al. 2019). It is recognized that high concentrations of monounsaturated fatty acids (MUFAs) and a lower melting point could amend the taste, texture and fat quality of the meat (Yang et al. 1999).

Findings on the incorporation of acetate and glucose into fatty acid synthesis in intramuscular adipose tissue show variable trends. Some studies indicate that glucose serves as a more active precursor than acetate in providing acetyl units for lipogenesis in bovine intramuscular fat (Smith and Crouse 1984). However, other studies, such as Matsuno (2014), have demonstrated that acetate stimulates key lipogenic enzymes, such as fatty acid synthase (FAS) and stearoyl-CoA desaturase (SCD), suggesting that acetate is also deeply involved in intramuscular fat formation and meat quality. Hood and Allen (1978) confirmed the hypothesis of the involvement of acetate in lipogenesis of intramuscular adipose tissue. They investigated the incorporation rate of acetate into CO₂ and fatty acids in the adipose tissue of four muscles (trapezius, longissimus dorsi, semi membranous and pectoralis profundus muscles). Among the mentioned muscles, the pectoralis profundus was more active in lipogenesis by using acetate as the precursor. Subcutaneous adipose tissue has larger adipocytes, consuming more acetate as a source of carbon in lipogenesis; consequently, subcutaneous adipose tissue is more active than muscle in fat synthesis.

In addition to the effects of acetate on carcass characteristics, butyrate and propionate also influence meat quality and marbling scores. Lean meat yield tends to decrease by rising the amount of propionate and butyrate (Bulumulla 2018). Propionate is a hepatic precursor for glucogenesis in ruminants. Therefore, it can be used in salt form with sodium or calcium to replace part of the energy provided by grains in diets (Lee-rangel et al. 2012). A moderate amount of propionate supplementation induces glucose flux (Van Houtert et al. 1993), fat synthesis and muscle growth in lambs. Cifuentes-López et al. (2018) found that feeding lambs with CaPr in their ration would elevate the yield of cold and hot carcasses and increase the conformation rate and area of the longissimus dorsi. However, excess CaPr supplementation decreases the fatness degree, pH of the meat and oleic acid synthesis in the longissimus muscle. Steers supplemented with CaPr in their diets tend to have less content of polyunsaturated fatty acids (PUFA) in their meat (Mendoza-Martínez et al. 2016). Moloney (1998) investigated the effects of the addition of NaPr at different rations (starch-based and sugar-mixture-based rations). The inclusion of propionate in the starch-based rations decreased the acetate-to-propionate ratio, causing an increase in muscle growth and regression in fat deposition. However, this was in contradiction with Abdul-Razzaq et al. (1988) findings, where they compared different isoenergetic diets with various ratios of acetate to propionate. They found that a decreased acetate-to-propionate ratio would cause an elevation in lipogenesis in the adipose tissue of muscle, which confirms the results of Ørskov and Allen (1966).

4 Sustainable approach to volatile fatty acids provision

In anaerobic digestion of organic waste and residues, VFAs are generated as precursors for biogas production. An AD bioreactor uses a mixed culture of microorganisms and resembles in function to the rumen. This section considers potential challenges and opportunities in sustainable production, recovery and application of organic waste/residue-derived VFAs as replacement for their fossil-based counterparts.

4.1 Organic residues for VFAs production

In order to take advantage of the benefits associated with the inclusion of VFAs in ruminant diets (Section 3), the sustainable provision of VFAs in economically feasible and environmentally friendly approach is of prime importance. Although VFAs are currently produced mainly from fossil sources, there is the potential to generate low-cost VFAs from organic residues and waste streams (Agnihotri et al. 2022). VFA production from low- or negative-value organic residues and waste to be used in ruminant feeding is considered as a waste management route fully complying with a circular economy concept, not only creating value but also enhancing resource efficiency (Lee et al. 2014; Agnihotri et al. 2022). The AD system resembles an external rumen in function and final metabolites. If methane production is inhibited in such stage-wise bioprocesses, intermediate metabolites such as VFAs, which are precursors to methanogenesis are accumulated and can be recovered (Figure 2). Owing to the simplicity, effectiveness and

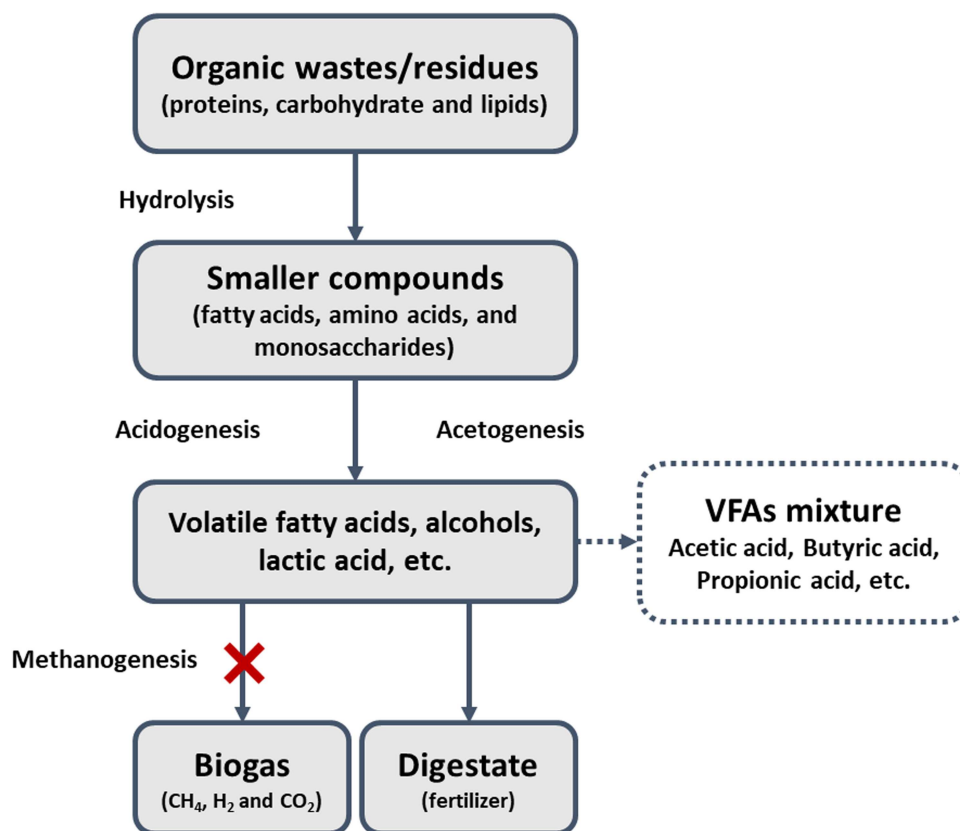


Figure 2. Different stages of anaerobic digestion for the production of VFAs from organic-rich residues/waste.

technical maturity of AD in handling organic waste, extensive research has been performed on VFA production via AD from a long list of organic-rich residues or waste streams. Table 2 presents a small collection of research conducted on VFA generation from organic-rich waste. This section looks into the potential of sustainable AD VFA production and recovery for animal feed supplementation.

Most common streams studied for VFA production include, food waste (FW) (Yin et al. 2016; Lukitawesa et al. 2019; Wainaina et al. 2020), waste activated sludge (Naresh Kumar and Venkata Mohan 2018; Huang et al. 2019; Wu and Song 2019), animal manure (Coats et al. 2011; Cavinato et al. 2017a), agricultural residues (Greses et al. 2020), effluent of palm oil mill (Lim et al. 2020) and dairy industry wastewater (Atasoy et al. 2020) (Table 2). FW is one of the most explored waste streams for VFA production, along with primary sludge and wastewater activated sludge originating at municipal wastewater treatment plants. The latter has been frequently investigated because of its enormous production across the globe from extensive use in biological wastewater treatment (Jiang et al. 2007).

Different parameters can influence the outcome of VFA production from waste streams. The main factors proven to impact VFA yield and concentration during AD are the nature of the substrate (protein, fat and carbohydrate contents and types), temperature, pH, inoculum, substrate-to-inoculum ratio, organic loading rate (OLR), hydraulic retention time (HRT) and other factors (Garcia-Aguirre et al. 2017; Wainaina et al. 2019a). As discussed in Section 3, the concentration and ratio of supplemented VFAs in the ruminant diet are highly important. By changing the combination of the above-mentioned factors during fermentation of organic wastes, different VFA titres, yields (0.1–0.8, as presented in Table 2) and ratios can be achieved (Wainaina et al. 2019a). Although it cannot be generalized, in most studies, AcA has been the dominant VFA, followed by BuA and PrA in alternating order. For instance, for VFA production from FW, Wainaina et al. (2020) reported a final VFA mixture containing around 40% AcA, 25% caproic acid and 24% BuA. However, if a different inoculum is used and the inoculum is heat treated to eliminate methanogens the final AcA fraction in the VFAs mixture derived from FW AD can rise to 66%–80% as recorded by Tampio et al. (2019). On the other hand, considering the organic fraction of municipal solid waste (OFMSW) as

Table 2. Different substrates used in anaerobic fermentation of VFAs, anaerobic digestion conditions and final yield, type and ratio of VFAs.

Substrate(s)	Anaerobic digestion (AD) condition (opt.)				VFA yield	VFA distribution	Ref.
	Mode	pH	Temp. (°C)	Period/HRT (day)			
Food waste	Semi-continuous	5.5	37	-	16.04 g/L	Acetic acid (39.52%) Caproic acid (24.94%) Butyric acid (23.60%) Acetic acid, butyric acid, caproic acid	Wainaina et al. (2020)
Food waste	Batch	6	37	14	-	0.8 g VFA/g VS _{added}	Lukitawesa et al. (2019)
Food waste	Batch	6	30	17	17.98 g/L	0.79 g COD/g VS	Yin (2016)
Food waste	Batch	7	35	11	11.8 g COD/L	-	Zhang et al. (2020)
Food waste	Batch	6	35	8	41.34 g/L	0.379 g VFA/g VS _{fed}	Jiang et al. (2013)
Food waste	Semi-continuous	6	35	5	13.27 g/L	0.504 g VFA/g VS _{fed}	Jiang et al. (2013)
Food waste	Batch	6	35	17	11.8 g COD/L	0.18 g COD/g VS _{added}	Xu et al. (2012)
Food waste	Batch	-	20	15	-	0.638 g COD/g VSS	Zhao et al. (2016)
Excess sewage sludge/ Food waste	Batch	12	37	25	14.73 (ESS) and 16.40 (FW) g/L	0.46 g VFA/g VS _{ESS} 0.56 g VFA/g VS _{FW}	Parchami et al. (2020)
Food waste/cow slurry	Batch	NC	37	10	5.4 (FW) and 2.5 (cow slurry) g/L	0.43 g VFA/g VS _{FW} 0.24 g VFA/g VS _{cowslurry}	Tampio et al. (2019)
Excess sewage sludge	Batch	NC	30	30	4.405 g COD/L	Acetic acid (66%–80%) Butyric acid (3%–20%) Propionic acid (3%–5%) for food waste	Iglesias-Iglesias et al. (2019)
Organic fraction of municipal solid waste	Semi-continuous	6	35	3.5	11.5 g VFA/L	Acetic acid (66%–71%) Propionic acid (17%–23%) Butyric acid (5%) for cow slurry	Cheah et al. (2019)
organic fraction of municipal solid waste	Batch	10	35	10	8.320 g COD/L	Acetic acid (35.27%) Propionic acid (22.05%) Butyric acid (19.79%)	Garcia-Aguirre et al. (2017)
Biowaste from biological treatment plant	Batch	NC	35	25	23.0 g COD/L	Acetic acid, propionic acid, butyric acid	Fernandez-Dominguez (2020)
Household biowaste	Batch	6	-	3	20.54 g/L	0.310 g VFAs/g VS _{fed}	Den Boer et al. (2020)

(Continued)



Table 2. (Continued)

Substrate(s)	Anaerobic digestion (AD) condition (opt.)						VFA yield	VFA distribution	Ref.
	Mode	pH	Temp. (°C)	Period/HRT (day)	OLR	Total VFAs			
Waste activated sludge	Batch	10	28	3	-	4.9 g/L	Acetic acid (5.8%) Propionic acid (0.8%) Acetic acid, propionic acid, butyric acid	Naresh Kumar and Venkata Mohan (2018)	
Waste activated sludge	Batch	NC	35	14	-	3.183 g COD/L	Acetic acid, propionic acid	Wu and Song (2019)	
Waste activated sludge	Batch	9	35	9	-	65.6 mg COD/g VSS	Acetic acid, propionic acid	Huang et al. (2019)	
Cow manure/Maize silage	Semi-continuous	NC	37	4	17.9 kg TVS/m ³ d	0.18 g COD/g VS _{feed}	Acetic acid (44%) Butyric acid (29%)	Cavinato et al. (2017)	
Manure	Batch	NC	20–21	6	40.7 g VS/L	0.103 g VFA as COD/g VS	Acetic acid (59%–74%) Propionic acid (16%–21%) Butyric acid (10%–17%)	Coats et al. (2011)	
Agro-industrial waste	Continuous	5.5–6.0	25	-	3 g VS/Ld	1.24 g COD/g VS _{influent}	Butyric acid (24.5%–43.5%) Acetic acid (24.7%–32.2%)	Gresses et al. (2020)	
Microalgae	Semi-continuous	NC	25	8	12 g COD/Ld	0.37 g COD/g COD	Butyric acid (23%–32%) Acetic acid (19%–26%)	Magdalena et al. (2019)	
Algae	Batch	6.5	55	5	-	2.07 g/L	Propionic acid (11%–17%) Acetic acid (54.2%) Butyric acid (29.6%)	Kim et al. (2019)	
Saccharification residue from FW ethanol fermentation	Batch	6.5	37	3	-	0.268 g COD/g VS	Propionic acid (14.6%) Butyric acid (79.3%) Propionic acid (9.4%) Acetic acid (4.6%)	Jin (2019)	
Potato peel waste	Batch	7	37	5	-	632.2 mg COD/g VS _{feed}	Iso-valeric acid (3.5%) Acetic acid, propionic acid, butyric acid	Lu et al. (2020)	
Palm oil mill effluent	SBR	5.13	29	5	6680 mg COD/Ld	10.5 g/L	Valeric acid (21.53%) Butyric acid (21.24%) Caproic acid (20.90%) Propionic acid (13.07%) Acetic acid (12.95%)	Lim et al. (2020)	
Brewers' spent grain	Fed batch	4.7	30	16	16 g TS/Ld	24.9 g/L	Propionic acid (41.3%) Acetic acid (28.2%) Butyric acid (17.2%) Valeric acid (9.6%) Iso-valeric acid (2.6%) Iso-butyric acid (1.0%)	Ribau Teixeira et al. (2020)	
Hydrothermal alkali pretreated tannery sludge	Batch	10	50	12	-	1037.5 mg/g sCOD	Acetic acid (63.1%), propionic acid, butyric acid	Zhai et al. (2020)	
Crude glycerol	Semi-continuous	5.5–6.0	35	1	-	-	Acetic acid, propionic acid, butyric acid	De Almeida Silva et al. (2020)	
Cheese processing wastewater	Batch	10	35	15	-	1993 mg COD/L 0.97 g VFA/g sCOD	Lactic acid, acetic acid, propionic acid, butyric acid	Atasoy et al. (2020)	

NC = not controlled.

feedstock for VFA production, Cheah et al. (2019) reported that the distribution of the main VFAs were 35.3% AcA, 19.8% BuA and 22% PrA. As presented in Table 2, just by manipulating the fermentation conditions during AD, the distribution of VFAs in the resulting effluent can be altered. Taking FW as an example, by changing the HRT and mode of AD operation from batch to semi-continuous, AcA (36.47%) was replaced by BuA (33.26%) as the main VFA.

A general conclusion on the best suitable organic residue or waste streams for VFA production cannot be drawn, as this is greatly influenced by the target application. While for some applications, such as cultivation of fungal single cell protein, a VFAs solution with a low total concentration of VFAs but rich in AcA compared to other VFAs is favoured (Uwineza et al. 2021), for supplementation of VFAs to specific ruminants lower AcA:PrA ratio may be considered as optimal (Moloney 1998).

Although VFAs can be sustainably generated from different types of organic residues and waste streams via AD, there are limitations on type of substrate, microbial inoculum and process used for animal feed grade VFA mixture provision.

VFAs may generally be categorized as nutritional feed additives than feed ingredient in animal feed regulations. In this context, the European Union has set clear guidelines on the type of feedstock and downstream and upstream processes used for the production of feed materials and additives in different regulations and directives, such as (EU) No 68/2013, (EU) No 142/2011, (EC) No 1069/2009 and (EC) No 1831/2003; Annex I (European Parliament and Council of the European Union 2022). Such regulations limit the choice of organic residue or waste used for VFA production for ruminants. For instance, cow manure may seem to be a potential substrate for sustainable VFA production, as it contains active microorganisms originating from the rumen that can be used for VFA production, contains undigested feedstuff with bioconversion potential, is generated in large amounts and is inexpensive; however, such animal by-products cannot be used in feed additive production for cows, as noted in (EC) No 1069/2009. Similar restrictions are in place for the application of ruminant by-products to produce ruminant feed materials or additives for the same species. For example, food waste, which is a heterogeneous organic waste with high potential for bioconversion to VFAs, is off the table as a substrate, as it may contain ruminant by-products such as meat, bone, or blood residues. However, the key to sustainable VFA provision may be the utilization of clean by-products or residues from the food, feed, forestry and agricultural industries, such as apple pomace (a residue from juice and cider production), potato protein liquor (a residue from potato starch production) and thin stillage (a by-product of the bioethanol production industry). In addition to the discussion put forward on substrate selection, the choice of microorganism used for VFA production is critical. Considering the application of anaerobic sludge, sewage sludge, manure, etc., for VFA production, although as presented in Table 2 is well-studied and optimized, there are regulatory limitations on the inclusion of the resulting metabolites as feed. One possible option here is to incorporate naturally occurring ruminal microbes in VFA production from organic residues. This could be possible by acclimatization and propagation of the microflora in the rumen fluid.

4.2 VFAs recovery and purification approaches

The AD effluent containing the desired VFAs contains components such as undigested particulate matter, microorganisms, minerals and chemical compounds that are unwanted when the VFA solution is applied in ruminant feed. VFAs obtained from anaerobic digestion of organic residue or waste streams are in a dissolved state in fermentation broth. As this mixed effluent contains impurities, it cannot be directly fed post-AD and needs to undergo certain separation and purification processes to be polished to feed grade. Various separation techniques, such as adsorption/ion exchange, distillation, precipitation, solvent extraction, electrodialysis, membrane separation, etc. have been used to extract these dissolved VFAs from different effluents. A comprehensive list of studies conducted on the separation, purification and concentration of VFAs from different effluent streams are presented in Table 3.

As most AD effluents have low VFA titres, the recovery step is challenging, adding to the total process cost (about 30% of total processing cost) (Murali et al. 2017). Therefore, an economically and technically feasible process needs to be established for the recovery of total and individual VFAs tailored for specific fermentation conditions (López-Garzón and Straathof 2014). Moreover, the choice of recovery method is challenged by the type of impurities present (Aghapour Aktij et al. 2020) and foreseen application for

Table 3. Case studies on separation, purification and concentration of VFAs from AD effluent.

Substrates	Separation approach	Materials used	Initial VFAs	Temp. (°C)	pH	Recovered VFAs	Recovery efficiency	Ref.
Wastewater	AD	Polystyrene-divinyl benzene-based resins	0.25–1.25 wt %	20–200	–	Acetic acid, butyric acid, propionic acid, lactic acid	Up to 93% for butyric acid and 89% propionic acid	Reyhantash et al. (2017)
Food waste	AD	Amberlite IRA-67 and activated carbon adsorbent	0.6–11.6 g/L	25	2–6	Acetic acid, lactic acid, butyric acid	Recovered between 63%–74% VFAs	Yousuf et al. (2016)
Landfill leachate	AD	Activated carbon		20–40	3	Acetic acid and butyric acid	Recovered up to 89.1% for acetic acid and 67.8% butyric acid	Talebi et al. (2020)
Grape pomace synthetic VFAs	AD	Amino ion exchange resins: Septra NH2, Amberlyst A21, Septra SAX and Septra ZT-SAX	19.1–19.8 g/L	20–22	2.5–7	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid, caproic acid	Amberlyst A21 yielded up to 88%	Rebecchi et al. (2016)
Synthetic VFAs and leachate	MC	Gas filled flat hydrophobic Polytetrafluoroethylene (PTFE) membrane	280–7800 mg/L	25	3–5.45	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid, caproic acid	Mass flux and selectivity of acetic acid 12.23 g/m ² h and 1.599 respectively	Tugtas (2014)
Synthetic VFAs and Organic solid waste	MC	Hydrophobic PTFE membrane	428–14277 mg/L	23	2.92–6.6	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	Increase in acetic acid fraction of leachate from 24.7%–43.0%	Yesil et al. (2014)
Synthetic VFAs and organic-rich waste	VPMC	Triethylamine (TOA) and Tridodecylamine (TDDA) extractant-filled PTFE and PTFE membranes	133–7885 mg/L	21–38	4	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	Acetic acid recovery of 45% and 86 to 95% for propionic acid, butyric acid and valeric acid	Aydin et al. (2018)
Synthetic VFAs	PV	PTFE, (TDDA) filled PTFE, composite silicone rubber/PTFE membranes	2 g/L each	21–55	3	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	VFAs selectivity 0.7–3.3	Yesil et al. (2018)
Waste activated sludge	MF and CED	Plyethersulfone microfiltration membrane, CED cell configuration ED 64–4 membrane stack with 20 cell pairs.	6.5–12 g/L	37	6–8.5	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid	80%–92% of VFAs of recovered VFAs concentration of 19.8 g/L achieved via MF/CED.	Tao et al. (2016)
Olive Mill wastewaters	ED	Homopolar membranes: Neosepta CMX and AMX	3900–14500 mg/L	20–30	3.5	Acetic acid, butyric acid, propionic acid	VFAs removals about 30%–35%.	Scoma et al. (2016)
Synthetic VFAs and Pig manure hydrolysate	ED	Cation exchange membrane (CEM), anion-exchange membrane (AEM) and bipolar membrane (BM)	9.54–10.03 g/L	–	5	butyric acid, iso-butyric acid, propionic acid, valeric acid, sodium acetate	Up to 95% of VFAs recovery	Shi et al. (2018)
Synthetic VFAs, Wastewater and pig manure	MBEDC	Bipolar membrane (BPM), Cation exchange membrane (CEM), anion-exchange membrane (AEM)	53.1 mM	22	3.3–12.6	Acetic acid, butyric acid, propionic acid	Up to 98.3% of VFAs recovered	Zhang and Angelidaki (2015b)
Wheat straw	Electrodialysis and distillation	Reverse electro enhanced dialysis (REED) and ED-bipolar membrane	–	30–37	5–7	Acetic acid, butyric acid	Up to 99% purity of butyric acid, and 89% purity for the mixture of butyric and acetic acids	Baroi et al. (2017)

Table 3. (Continued)

Substrates	Separation approach	Materials used	Initial VFAs	Temp. (°C)	pH	Recovered VFAs	Recovery efficiency	Ref.
Agriculture wastewater	NF	NF270, HL, DL, DK and LF10 NF membranes	50–100 mM/L	40–50	4–9	Acetic acid, butyric acid	Retention ratio up to 75% with retentates up to 53.94 mM acetic acid and 28.38 mM butyric acid	Zacharof et al. (2016)
Willow wood digestion liquor	NF	Desal DK and Desal DL FW membranes, integrated dead-end NF	0.1–30 g/L	25	3–7	Acetic acid, butyric acid, propionic acid, formic acid, lactic acid, caproic acid	Up to 100% butyric rejection. Up to 86% of acids was recovered	Xiong et al. (2015)
Synthetic VFAs and domestic wastewater	NF	ES10 and NF270 membranes	49 mg/L	25	3.4–6.6	Formic acid, acetic acid, propionic acid, succinic acid, citric acid	Up to 90% of rejection	Choi et al. (2008)
Food waste	MF	Immersed Flat sheet membrane panel	–	37	Initial pH 6	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid, caproic acid	Recovered between 3%–47% VFAs	Wainaina et al. (2019b)
Food waste and excess sewage sludge	MF	Immersed Flat sheet membrane panel	–	37	Initial pH 5	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid	ESS: 3%–53% VFAs recovered FW: 3%–42.63% VFAs recovered	Parchami et al. (2020)
Dewatered sewage sludge	MF	0.1 µm hollow fibre membrane	14 g/L VS	25	Initial pH 9	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid	Up to 74% rejection rate of VFAs	Gao et al. (2019)
Liquid sludge	MF	Ceramic membranes with pore size ranging between 0.1–5 µm	–	35	5–6	Mixed VFAs	Up to 65%–86% VFAs recovered in permeate	Kim et al. (2005)
Rumen fluid and maize silage	UF	0.04 µm hollow fibre membrane	–	39	–	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid, caproic acid	VFAs removal over 73 ± 15%	Nguyen et al. (2020)
Sludge and synthetic wastewater	AnMBR and SOLE	0.07–0.1 µm hollow fibre membrane and methyl tert-butyl ether (MTBE) solvent	–	22	5–12	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid, caproic acid, iso-caproic acid, enanthic acid	Highest yield of 48.74 ± 1.5 mg VFA/100 mg COD feed	Khan et al. (2019)
Sewage sludge and molasses wastewater	Dynamic MBR	Silk an aperture of with 0.1 mm separation layer	1.0 ± 0.1 g/L	37	10	Acetic acid, butyric acid, iso-valeric acid	Up to 60 g/L of VFAs	Liu et al. (2019)
Waste sludge	Self-forming dynamic membrane	Silk an aperture of with 0.1 mm separation layer	–	35	10	Acetic acid, butyric acid, propionic acid	VFAs yield increased up to 61.21%–221.8%	Liu et al. (2016)

(Continued)

Table 3. (Continued)

Substrates	Separation approach	Materials used	Initial VFAs	Temp. (°C)	pH	Recovered VFAs	Recovery efficiency	Ref.
Perennial grass and synthetic medium	PV	Polymer block amides (PEBA): Graphene, graphene oxide and molybdenum sulphide membranes	7.3 g/L	40–70	3.7–7	Butyric acid	Yielded up to 24.3 g/m ² h of mass flux with a separation factor of 21. The butyric acid content increased up to 19-times	Choudhari et al. (2015)
Diluted alginate solution	SOLE and DIS	Nonyl acetate and hexyl acetate solvents	9.8 g/L	30–232	–	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	Product recovery of 98% for acetic acid and 99% for propionic acid. Acid purity was 99.5%	Woo and Kim (2019)
Organic municipal waste	Percolation, LLE	Ethanol and biodiesel as solvent	22 ± 6 g/L	30–45	3	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid, enanthic acid, caprylic acid	The extraction efficiency between 0.5%–6.5% for acetic acid and propionic acid and 50%–100% for others	Kannengieser et al. (2016)
Dilute aqueous solutions of single acids	LLE and DIS	Phosphine based extractant (Cyanex 923 and mineral oil) and trioxylamine (TOA) extractant	5–30 g/L	–	2–6	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	Up to 100% of acetic acid and butyric acid recovered by distillation and 91.6% for TOA and 71.2% for cyanex 923 of caproic acid	Saboe et al. (2018)
Sugar industry wastewater and beet-pulp	LLE	Trioctyl-phosphine oxide (TOPO) use as extractant solvents and kerosene as diluent	2910 ± 20 mg/L	30	2.5–5.5	Acetic acid, butyric acid, propionic acid, iso-butyric acid, valeric acid, iso-valeric acid, caproic acid	Highest VFAs recovery up to 98% was achieved.	Alkaya et al. (2009)
VFAs solution in water	LLE	Hexanoic, octanoic and decanoic acids as extractants. <i>N</i> -hexane and toluene as diluents	1 wt%	RT	7.3	Acetic acid, butyric acid, propionic acid	Caproic acid and toluene resulted in better extraction efficiency up to 80%.	Rocha et al. (2017)
Ethanol fermentation broth	LLE	Ethyl acetate (EtOAc), TOPO, TOA and tri-alkylphosphine oxide (TAPO)	20 g/L	25	–	Acetic acid	TAPO and TOPO yielded 97% and 92.4% respectively.	Pham et al. (2015)
Synthetic VFAs, thin stillage broth	RE	TOA, tri- <i>n</i> -butyl phosphate (TbP), aliquat 336, <i>N</i> -methyl-diethylamine and TOPO	0.2–22 g/L	RT	4.5–5.5	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	Up to 75%–85% VFAs extraction efficiency	Kaur et al. (2020)
Swine manure	DAS	Air stripping	39.1 mg-COD/g-VS	35–55	8–10	Acetic acid, propionic acid, iso-valeric acid	94.4 mg-COD/g-VS of Total VFAs achieved	Huang et al. (2016)
Thin stillage	Membrane-based RE	LiquiCel hollow fibre and TOA, TbP, Aliquat 336, <i>N</i> -methyl-diethylamine and TOPO	5.5–22 g/L	22	4.5–5.5	Acetic acid, butyric acid, propionic acid, valeric acid, caproic acid	Up to 15%–100% VFAs extraction	De Sitter et al. (2018)

Note: RT = room temperature, ED = electro dialysis, AD = adsorption, MC = membrane contactor, VPMC = vapour permeation membrane contactor, CED = conventional electro dialysis, PV = pervaporation, MBEDC = microbial bipolar electro dialysis cell, DIS = distillation, AnMBR = anaerobic membrane bioreactor, LLE = liquid–liquid extraction, LLE = liquid–liquid extraction, MF = microfiltration, UF = ultrafiltration, NF = nanofiltration, RE = reactive extraction, DAS = dry ammonia stripping.

recovered VFAs (Atasoy et al. 2018). The choice of VFA purification process is further strained when VFAs are to be used as animal feed supplements. The separation and purification in this case should not involve chemicals other than those certified as feed grade and should not create an imbalance between the product and its effect.

Separation and purification techniques can be implemented either *in situ* or post fermentation (downstream) (Wainaina et al. 2019a). As the removal of VFAs during AD is critical for microbial health and fermentation progression (Yang et al. 1991; Cheng et al. 2010), VFAs are continuously removed from fermentation broth (*in situ*) (Yesil et al. 2018). Here, the most common methods used for the separation, purification and concentration of VFAs have been reviewed in brief.

Electrodialysis (ED) is a separation method used to recover carboxylic acids using an electrical field as a driving force to send ions towards electrodes as they are being isolated through semipermeable membranes (Khan et al. 2018). As presented in Table 3, ED has been applied successfully for VFA separation from fermentation media. Although ED can provide high-purity acids without the requirement of medium pH adjustment, it has challenges in terms of processing cost, scale-up and VFA concentration limit (Huang et al. 2007; Tao et al. 2016; Murali et al. 2017).

Another well-practiced technique used for the recovery of VFAs is adsorption, which is categorized as a surface-based affinity separation method. This method can be applied for effluents with low VFA contents, such as fermented wastewaters (Reyhanitash et al. 2017). During adsorption, the interaction between acids in ionic form and the adsorbent causes the retrieval of dissolved VFAs (Da Silva and Miranda 2013). This is then followed by a desorption stage, where VFAs (adsorbates) are detached and the adsorbent is recovered. Adsorption-based methods such as ion exchange are simple, cost effective and relatively selective but may be challenged by poor desorption (Rasrendra et al. 2011; Rebecchi et al. 2016; Reyhanitash et al. 2017).

Distillation is a well-developed and featured industrial process for the separation of compounds based on their volatility. VFAs have a carboxyl group as an electrophile, giving them a higher boiling point than that of water. This provides the opportunity to separate VFAs from water rather easily in dilute VFA effluents (Aghapour Aktij et al. 2020) through distillation. Although this technique provides a high-purity VFA product stream and has been successful in low-content VFA streams, it loses effectivity with solutions bearing high VFA contents and is highly demanding in terms of energy and cost (Huang et al. 2008; Errico and Rong 2012; Aghapour Aktij et al. 2020).

Another *in situ* separation method functioning based on the difference in the solubility of VFAs in two non-miscible solvents is solvent extraction. As this method is economical and efficient, has a low energy demand, and is associated with a high product recovery yield, it has been applied in the separation of VFAs from different media. However, the application of this separation technique is hindered by the application pH range (poor VFA recovery at high fermentation pH (Murali et al. 2017)), regeneration of solvents and recovery of extractants (Kurzrock and Weuster-Botz 2010; Rasrendra et al. 2011; Ijmker et al. 2014; Li et al. 2016; Reyhanitash et al. 2017; Rocha et al. 2017). The results of several investigations on liquid-liquid extraction for VFA recovery are cited in Table 3.

Precipitation is another classic separation method used for the separation of carboxylic acids from AD media (Berglund et al. 1999; Min et al. 2011). This recovery process is highly selective and yields a high-purity product with no phase transition involved, though rather costly and generates its own solid waste (Min et al. 2011; Li et al. 2016; Tao et al. 2016).

Among the popular methods applied for the separation and purification of VFAs from AD effluent are membrane separation techniques. Membrane separation is a physical filtration method that is considered environmentally friendly, has a low energy demand and is economically feasible for the recovery of VFAs (Trad et al. 2015). Membranes are defined as semi-permeable barriers between two phases and are made mainly from polymers, ceramics and metals and use pressure, concentration, partial pressure or electric potential gradient over the membrane as the driving force for the separation of compounds (Mahboubi 2019). The most commonly applied membrane techniques for impurity removal and VFA recovery have been pressure-driven filtration methods such as microfiltration (MF), ultrafiltration (UF), nanofiltration (NF), reverse osmosis (RO), or non-pressure-driven processes pervaporation (PV), electrodialysis (ED), membrane distillation (MD) and a membrane contactor (MC) (He et al. 2012). A collection of literature concerning the application of the membrane separation technique in VFA recovery is presented in Table 3. Membrane separation enjoys modularity, ease of upscaling while being eco-friendly and cost effective; however,

membrane fouling challenges the expansion of the membrane separation market (Defrance et al. 2000; Bae and Tak 2005; Tugtas 2014; Trad et al. 2015; Aghapour Aktij et al. 2020).

5 Future prospects

As discussed in detail in previous sections, the effect of VFA addition to ruminant diets in either salt or acid forms has been investigated for approximately 70 years. This has led to the discovery of the spectrum of VFA effects on ruminant physiology, metabolism and products. Although the advantages gained by VFA administration are dominant, in many areas, a consensus on the effects has not been reached. Therefore, to determine the full potential of VFAs in ruminant feed and to standardize the rules and routines regarding the inclusion of VFAs in ruminant diets, extensive future research is pivotal.

Moreover, as the world is ever more veering towards sustainable and circular practices in food and feed provision, obtaining VFAs should adopt such approaches in order to guarantee their long-term role in ruminant feed. In this context, fossil-derived VFAs may not have a place in this future picture. A sustainable approach that fully falls under the circular economy umbrella is the bioconversion of organic residues to VFAs. Using industrial residues and ruminal microorganisms for the fermentation of ruminant feed additives such as VFAs will realize the 'less is more' goal by not only reducing the resources used and reducing the volume of residuals generated but also providing animal feed and creating value.

6 Conclusions

Volatile fatty acids, as naturally generated metabolites in the rumen of ruminants, are important, mainly because the microbial bioconversion of carbohydrates has an essential role in supplying metabolizable energy for ruminants in addition to their effects on animal products. The inclusion of individual or mixtures of VFAs at different concentrations and ratios, in acidic or salt form, administered either orally, intravenously or in dry matter, such as in ruminant diets, has been proven to directly or indirectly affect animals' gastrointestinal development, weight gain, dry matter intake, blood hormone levels, milk yield and composition, meat quality, adipose tissue and more in various ways. By proper dosing of VFAs, the associated advantages can be harvested to benefit ruminant health and physiology while increasing the amount or quality of animal products. Sustainable provision of the required VFAs can be achieved through anaerobic digestion of organic-rich, low value residuals and by-products followed by further VFA-rich effluent polishing through separation, purification and concentration downstream processing. Through this approach value creation from residues is maximized by converting the wasted nutrients into ruminant feed additive in an environmentally friendly, economically feasible sustainable practice.

Endnote

1. Hungate, *The Rumen and Its Microbes*.

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