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Review

Anaerobic co-digestion: Current status and perspectives

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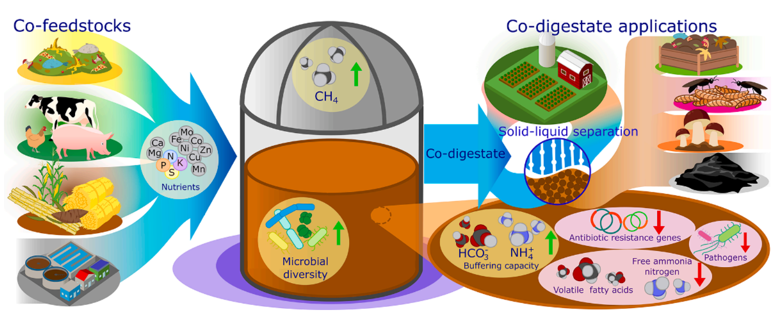
HIGHLIGHTS

- Anaerobic co-digestion can overcome the drawbacks of mono-digestion.
- Usage of diverse feedstocks have different effects on co-digestion stability.
- Feedstock characterization is crucial for process efficiency.
- In-depth microbial analyses need to be conducted.
- Kinetic models for co-digestion need to be improved.

GRAPHICAL ABSTRACT



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ABSTRACT

Anaerobic digestion is a long-established technology for the valorization of diverse organic wastes with concomitant generation of valuable resources. However, mono-digestion (i.e., anaerobic digestion using one feedstock) suffers from challenges associated with feedstock characteristics. Co-digestion using multiple feedstocks provides the potential to overcome these limitations. Significant research and development efforts have highlighted several inherent merits of co-digestion, including enhanced digestibility due to synergistic effects of co-substrates, better process stability, and higher nutrient value of the produced co-digestate. However, studies focused on the underlying effects of diverse co-feedstocks on digester performance and stability have not been synthesized so far. This review fills this gap by highlighting the limitations of mono-digestion and critically examining the benefits of co-digestion. Furthermore, this review discusses synergistic effect of co-substrates, characterization of microbial communities, the prediction of biogas production via different kinetic models, and highlights future research directions for the development of a sustainable biorefinery.

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1. Introduction

Anaerobic digestion (AD) has gained wide acceptance for organic waste remediation coupled with energy production (biogas) and nutrient recovery (digestate). It is estimated that 50 million micro-digesters (2–10 m^3) are currently in operation worldwide for the sole purpose of generating biogas for cooking, heating, or lighting (WBA, 2019). Additionally, about 132,000 small (<1,000 m^3), medium (1,000–10,000 m^3), and large-scale (>10,000 m^3) digesters are currently in operation around the world, which approximately generate 87 TWh of electricity (Lindkvist and Karlsson, 2018; WBA, 2019). Over 18,202 AD plants in Europe and 2,200 in the United States are employed with installed capacities of about 11,000 and 977 MW, respectively (EBA, 2019; American Biogas Council, 2018). Despite widespread adoption of AD technology, only 1.6–2.2% of the total energy production potential of AD has been harnessed from available feedstocks (WBA, 2019).

Currently, many AD plants utilize mono-digestion systems (i.e., AD systems using one feedstock). However, there are substantial drawbacks of mono-digestion such as digester instability (Li et al., 2018b), limited year-round availability of some feedstocks (Mata-Alvarez et al., 2014), presence of heavy metals (Neshat et al., 2017), and low biogas/methane yield (Zahan et al., 2018). For instance, readily biodegradable organic waste streams (e.g., some food wastes) result in rapid accumulation of high concentrations of volatile fatty acids (VFA) in digesters inhibiting methanogens (Li et al., 2018b). On the other hand, high proteinaceous wastes (e.g., slaughterhouse waste) and sulfate-rich wastewater can result in the generation of toxic compounds such as ammonia (NH_3) and hydrogen sulfide (H_2S), respectively (Mu et al., 2020). These issues can be resolved to some extent by adjusting the pH (via alkali supplementation) (Zapata Martínez et al., 2019), controlling the retention time (hydraulic retention time equals solids retention time for most anaerobic digesters) (Vanwonterghem et al., 2015), feeding intermittently (Bonk et al., 2018), adopting micro-aeration (Nguyen et al., 2019), and using a two-stage AD system (Rajendran et al., 2020). Furthermore, the addition of microbial cultures (Aydin, 2016) and biochar (Masebinu et al., 2019) can sometimes enhance performance by adding missing microbial diversity, maintain high biomass, and reduce inhibitory effects. However, these modifications entail operational complexity and additional costs.

Anaerobic co-digestion provides an opportunity to overcome the drawbacks of mono-digestion by simultaneously digesting two or more feedstocks. Of the 1,200 water resource recovery facilities with AD in the United States, approximately 133 have incorporated co-digestion by adding organic waste streams such as food waste or high strength industrial byproducts (e.g., glycerin) to sewage sludge (Jones et al., 2019). The major benefits of co-digestion include enhanced system stability and methane yield through the synergistic effects of promoting a more diverse microbial community (Mata-Alvarez et al., 2014), better nutrient balance (proper carbon-to-nitrogen (C/N) ratio and supplementation of trace elements) (Xie et al., 2018), improved buffering capacity (Bolzonella et al., 2006a), dilution of toxic compounds including heavy metals (Ebner et al., 2016), safe and better quality digestate for agricultural applications (Alburquerque et al., 2012), and reduction of antibiotic resistance genes (ARGs) and antibiotic resistant bacteria (ARB) (Zhang et al., 2018). Moreover, co-digestion increases the bioavailability of nutrients in the co-digestate (digestate from co-digestion) when used for composting (Bustamante et al., 2012), vermicomposting (Rékási et al., 2019), mushroom cultivation (O'Brien et al., 2019), and black soldier fly (BSF) farming (Elsayed et al., 2020; Surendra et al., 2020). The co-digestate can also be used for producing macronutrient-rich biochar for agriculture applications (Xie et al., 2018).

Despite numerous benefits of co-digestion, antagonistic effects due to incompatible feedstock mixing ratio can result in organic overloading, acidification, and system failure (Chow et al., 2020). These challenges, however, can be addressed by characterizing heterogeneous organic compounds in digester feedstocks and understanding their intrinsic biodegradability patterns (Hagos et al., 2017).

The few critical reviews available on co-digestion focus on either process engineering (Xie et al., 2018), microbial community structure (Xu et al., 2018b), or feedstocks (Mehariya et al., 2018; Nghiem et al., 2017; Tyagi et al., 2018) separately. Therefore, a critical review on co-digestion with a holistic focus on enhancing process performance and co-digestate utilization for sustainable AD biorefinery is needed. This review critically evaluates the feasibility of the practical implementation of co-digestion systems based on operational conditions, kinetic modeling, and nutrient recovery. This review further suggests compatible co-feedstocks for organic waste management and recommends practical steps for future research directions.

2. Merits of co-digestion

2.1. Digester stability and synergistic effect

Anaerobic co-digestion can result in synergistic interactions via balance of nutrients, supplementation of trace elements, dilution of toxic and inhibitory compounds, and promotion of microbial diversity as shown in Table 1. Previous studies have shown that a balanced C/N ratio achieved through co-digestion of different feedstocks prevents the accumulation of VFA due to an improved buffering capacity despite higher organic loading rate (OLR) (Wang et al., 2014; Zhang et al., 2011). For example, co-digestion of food waste with trace element-rich piggery wastewater can avoid VFA accumulation, resulting in process stability and improved methane production rates (Wang et al., 2020). Food waste is deficient in trace elements, which play an important role in activating enzymes (e.g., carbon monoxide dehydrogenase, coenzyme M-methyltransferase complex, and coenzyme F_{430}) (Mu et al., 2020) needed for the growth of syntrophic bacterial communities and methanogens. The nutrient balance and trace element (e.g., Fe, Ni, Co) supplementation by piggery wastewater can enhance microbial diversity and enzyme activities, and support symbiotic and syntrophic associations (Wang et al., 2020).

A reduction in inhibitory compounds, such as total ammonia nitrogen (TAN) (Li et al., 2018a), lignin derivatives (e.g., phenolic acids and eugenol) (Masih-Das and Tao, 2018), and furan (Adarme et al., 2019) was observed through the dilution effect of co-digestion in laboratory-scale experiments. However, the effect of adopting co-digestion in reducing the level of inhibitory compounds in full-scale applications still needs to be studied.

The co-digestion performance index (CPI) or synergistic index is used to evaluate antagonistic (CPI < 1), additive (CPI = 1), and synergistic (CPI > 1) interactions in co-digestion. CPI is defined as the specific methane yield (SMY) from co-digestion divided by the weighted average of SMYs from the mono-digestion of each feedstock (Ebner et al., 2016). While used as a performance indicator, a high CPI value does not guarantee a maximum SMY (Ebner et al., 2016; Kim et al., 2019b); thus, both SMY and CPI must be considered to identify the optimal mixing ratio of co-feedstocks.

CPI ranges, mixing ratios, and maximum SMYs from several studies are plotted in Fig. 1 to illustrate these concepts. Co-digestion of food waste (>50% volatile solids (VS)) and cellulosic feedstocks (i.e., spent coffee grounds, toilet paper, and *Sophora flavescens* residues) resulted in lower CPI values (1.05–1.30) than other co-feedstocks (i.e., pig manure, corn stover, cucumber residues, etc.) due to higher SMY of food waste mono-digestion (Kim et al., 2019a, 2019b; Ma et al., 2019; Ebner et al., 2016; Wang et al., 2018). In other studies, the co-digestion of animal manure and sludge with agricultural residues resulted in a CPI of around 2.0, which was associated with the supplementation of nutrients and trace elements, resulting in increased microbial diversity (Wang et al., 2018; Wei et al., 2020; Zhao et al., 2018; Okoro et al., 2018). Since CPI is a useful tool and only batch tests have so far been performed to evaluate this concept, a continuous-flow experiment should be conducted to

Table 1
Effect of different parameters that influenced batch co-digestion systems.

Co-feedstock	Operating conditions		SMY (mL g^{-1} VS_{added})	C/N	Synergistic effect			Reference
	ISR (VS basis)	Mixing ratio			VS reduction	CPI	Remarks	
Food waste: Dairy manure	2 (% w/w fixed)	UDG:DM 3:7	372	NA	NA	1.2	Dilution of inhibitory compounds such as VFA	Ebner et al., 2016
		FSB:DM 3:7 (% w/w fixed)	466			1.1		
Pig manure: Corn stover: Cucumber residues	0.6	5:1:4	~278	13.8	NA	1.9	Lower VFA/TA and hemicellulose content	Wang et al., 2018
		5:2:3	305	14.5		1.9		
Wet hydrolyzed DAF Sludge: Stock yard	2	1:4 (VS basis)	264	15.0	NA	1.8	Dilution of inhibitory compounds	Okoro et al., 2018
Oat straw: Cow manure	NA	2:1 (TS basis)	416	26.4	54	~ 1.5	VS reduction corresponding to SMY at TS_{feed} (%) of 4	Zhao et al., 2018
Food waste: *Sophora flavescens* residue	4	1:1 (VS basis)	629 (biogas)	27.3	58	1.2	Higher biogas in co-digestion compared to food waste mono-digestion	Ma et al., 2019
Food waste: Spent coffee grounds	0.5 (v/v)	67:3 (VS basis)	535	16.0	NA	1.3	Response surface analysis; predicted maximum SMY of 547 mL g^{-1} VS_{added} (FW: SCG = 76.3:23.7) and CPI of 1.34 (FW: SCG = 73.1:26.9)	Kim et al., 2019b
Food waste: Toilet paper	0.5 (v/v)	67:3 (VS basis)	~540	19.0	NA	~1.0	No substantial synergistic or antagonistic effect	Kim et al., 2019a
Crop residues: Sugarcane scum	0.5	3:1 (VS basis)	276	37.0–75.0	77	1.1	Higher SMY, VFA degradation, and VS removal	Mendieta et al., 2020

ISR: Inoculum to substrate ratio; SMY: Specific methane yield; CPI: Co-digestion performance index; COD: Chemical oxygen demand; BMP: Bio-methane potential; LFD: Liquid fraction of digestate; FW: Food waste; DM: Dairy manure; FSB: Food service blend; UDG: Unsweetened dry goods; WAS: Waste activated sludge; DAF: Dissolved air floatation; PM: Pig manure; MLSS: Mixed liquor suspended solids; VFA: Volatile fatty acids; TA: Total alkalinity; NA: Not available.

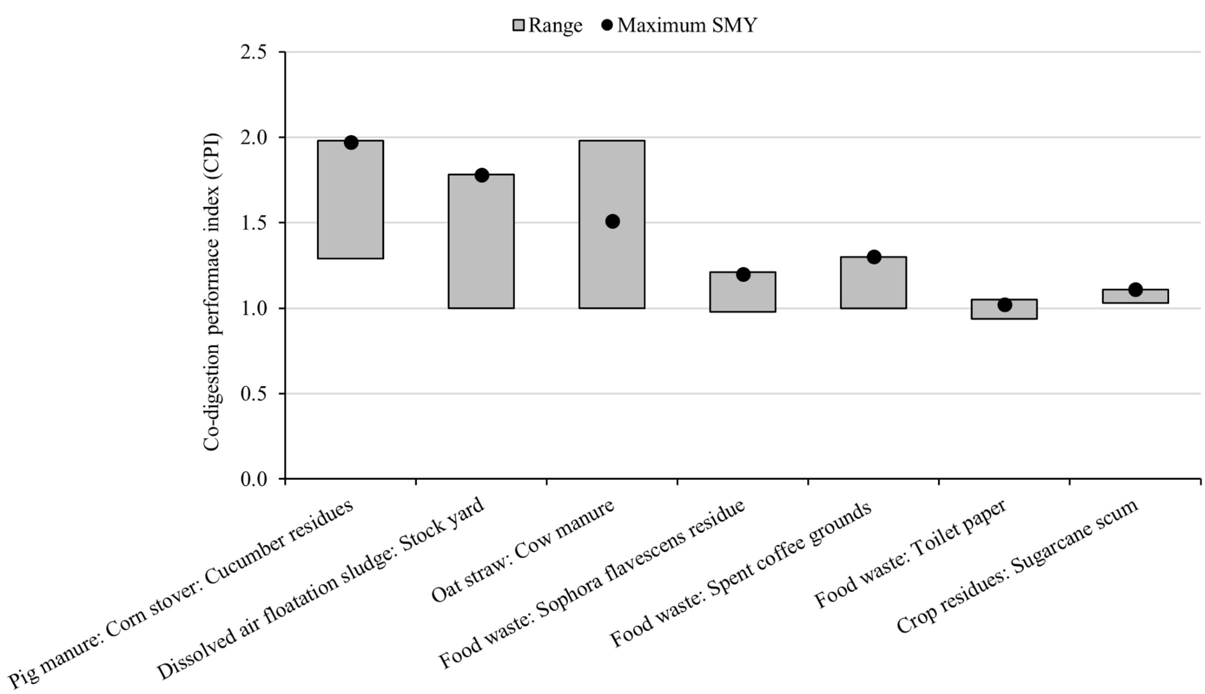

Fig. 1. Maximum specific methane yield (SMY) and co-digestion performance index (CPI) ranges of various co-feedstocks (Note: The data used for this figure were obtained from different literature studies discussed in Section 2.2).

better understand the synergistic effect due to co-feedstocks.

2.2. Microbial supplementation

Co-feedstocks that contain microbial populations relevant for anaerobic digestion continuously contribute to maintain diverse microbial communities during long-term co-digestion and have the potential to address concerns with microbial washout. In a co-digestion study with pig manure and food waste, an increasing proportion of pig manure resulted in a higher Shannon diversity index for methanogenic populations, especially at shorter retention time (Dennehy et al., 2018). The high diversity index was associated with a decreased risk of digester instability (Li et al., 2014). However, this is in contrast with findings from the co-digestion of sewage sludge with food waste, grass clippings, and garden waste at two different ratios of 10:67:16:7 and 5:22:16:7 (VS basis) at different retention times (Fitamo et al., 2017). While the decrease in retention time led to an increase in microbial diversity in the former combination, the latter combination resulted in a decreased microbial diversity but led to a selection of a robust lignocellulose-degrading microbial community, thus maintaining better digester stability.

Hence, the stability of microbial communities can be significantly enhanced via co-digestion of complementary feedstocks. Microbial supplementation through the addition of co-feedstocks is further discussed in Section 4.

2.3. Nutrient recovery

AD helps to transform complex organic compounds in the feedstocks into plant nutrients when digestate is used in agriculture. However, the application of digestate derived from mono-digestion (mono-digestate) of feedstocks such as animal manure and sewage sludge poses several environmental problems, including heavy metal accumulation, increased soil salinity, phytotoxicity, and ecotoxicity. These concerns can potentially be addressed through co-digestion (Kupper et al., 2014; Kataki et al., 2017; Xu et al., 2018b).

The addition of at least 30% sweet potato (dry weight basis) to dairy cattle manure led to an increase from 13.5% to 22.9% and 5.8% to 8.3% of N and K in the co-digestate, respectively (Montoro et al., 2019). Furthermore, Kataki et al. (2017) reported that co-digestate contained higher concentrations of Ca, S, Cu, Mo, Ni, Mn, and Zn than mono-digestate. Variability in the nutrient composition of digestates remains a major hurdle in accurately predicting the quality of digestate as a soil amendment, suggesting that this topic deserves further research.

2.4. Reduction of antibiotic resistance genes and antibiotic resistant bacteria

ARGs and ARB pose a severe threat to the environment and human health (Guo et al., 2020). The increase in abundance of ARGs and ARB in effluents and mono-digestate was attributed mainly to horizontal gene transfer mediated by mobile genetic elements such as plasmids, integrons, and transposons (Aydin et al., 2015). Since *Bacteroidetes*, *Firmicutes, Actinobacteria,* and *Proteobacteria* are mainly associated with ARGs, a shift in their relative abundances can result in the attenuation of ARGs (Guo et al., 2020; Song et al., 2017; Zhang et al., 2018). This effect was evident during the co-digestion of swine manure with wheat straw, where a decline in *Firmicutes*, *Bacteroidetes*, and *Actinobacteria* and an increase in *Proteobacteria* resulted in the attenuation of ARGs (Song et al., 2017). Paradoxically, an increase in *Actinobacteria* has also been associated with the attenuation of ARGs (Guo et al., 2020; Zhang et al., 2016). These opposing results may be valid because it is not always clear which bacterial groups carry relevant ARGs. As studies have reported significant effects of feedstocks on microbial community shifts (Guo et al., 2020; Zhang et al., 2018), selecting appropriate co-feedstocks could be one of the strategies to reduce ARGs and ARB levels. However, the influence of co-feedstocks and the underlying mechanisms supporting such reductions of ARGs and ARB would need to be further studied.

3. Co-feedstocks for co-digestion

3.1. Food waste

There is significant interest in the AD of food waste due to its high biodegradability and nutrient contents. Mono-digestion of food waste (carbohydrate: 12–74%, protein: 14–18%, and lipid: 4–34%, dry weight basis) generates a SMY that varies widely due to variation in feedstock compositions and operational conditions with a maximum SMY of around 460 mL g^{-1} VS_{added} (Fig. 2.) (Bong et al., 2018). The trace elements in food waste such as Ni (0.4–7.0 mg L^{-1}), Co (0.0–0.4 mg L^{-1}), Mo (0.05–0.11 mg L^{-1}), Fe (7.0–230 mg L^{-1}), and Se (0.05–0.60 mg L^{-1}) are inadequate for efficient mono-digestion (Xu et al., 2018a). Furthermore, a major drawback of food waste mono-digestion is the rapid hydrolysis rate, resulting in pH drop below 5.5 due to VFA accumulation (Bong et al., 2018). Hence, co-digestion of food waste with recalcitrant feedstocks can help slow down the hydrolysis rate and reduce the accumulation of VFA.

Co-digestion performance with >50% (w/w) food waste was evaluated in various studies, as summarized in Table 2. This summary indicates that co-digestion of food waste can be achieved effectively with around 70% of food waste (VS basis) for both sewage sludge and animal manure co-feedstocks. Co-digestion of food waste with sewage sludge or animal manure is beneficial due to micronutrient and alkalinity

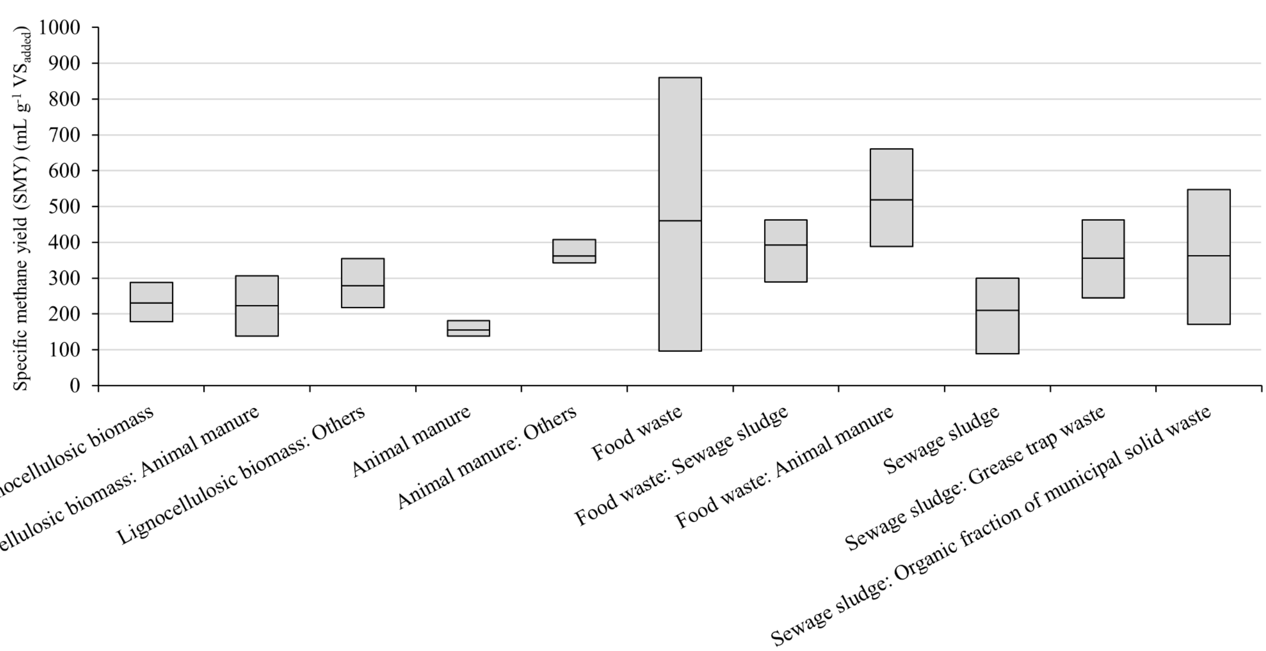

Fig. 2. Comparison of specific methane yield (SMY) range of mono- and co-digestion studies using various feedstocks (Note: The data for this figure were obtained from different studies summarized in Section 3).

Table 2
Studies on co-digestion of food waste.

Co-feedstock	Mixing ratio	Conditions	C/N ratio	OLR (kg VS m^{-3} d^{-1})	SRT (days)	SMY (mL g^{-1} VS_{added})	$VS_{reduction}$ (%)	Remarks	Reference
Food waste: Dewatered sludge	1:0.4 (VS)	Lab-scale	10–13	12.5	12	352	65	Low VFA, TAN but high FAN	Dai et al., 2013
Food waste: Sewage sludge	7:3 (TS)	Pilot-scale	9–10	2.4	25	449	64	No inhibition	Borowski et al., 2018
Food waste: Fruit and vegetable waste: Sewage sludge	2:1:1 (w/w)	CSTR Pilot-scale	NA	4	33	421	> 60	No inhibition At OLR of 8 kg VS $m^{-3}d^{-1}$, methanogenesis was rate-limiting step	Sun et al., 2013
Food waste: Sewage sludge	7:1 (NA)	Pilot-scale	NA	8.7 (kg COD m^{-3} d^{-1})	24	~289	70	No inhibition	Ratanatamskul et al., 2015
Food waste: Chicken manure	2:1 (VS)	CSTR Lab-scale	7–14	2.5	35	508	NA	No significant difference in SMY of co-digestion and mono-digestion	Wang et al., 2014
Food waste: Chicken manure	7:3 (VS)	CSTR Bench-scale	20	4	17	660	63	About 88% higher SMY during co-digestion than mono-digestion of food waste Optimum VFA/TA at OLR of 4 kg VS m^{-3} d^{-1} for co-digestion while VFA accumulation for mono-digestion	Chuenchart et al., 2020
Food waste: Dairy manure	2:1 (NA)	CSTR Lab-scale	16	12	NA	388	NA	About 4-fold increase in SMY during co-digestion compared to mono-digestion of food waste	Zhang et al., 2013

C/N: Carbon-to-nitrogen; OLR: Organic loading rate; SRT: Solids retention time, which equals the hydraulic retention time for most anaerobic digesters; SMY: Specific methane yield; VS: Volatile solids; TS: Total solids; COD: Chemical oxygen demand; VFA: Volatile fatty acid; TAN: Total ammonia nitrogen; TA: Total alkalinity; FAN: Free ammonia nitrogen; CSTR: Continuous-stirred tank reactor; NA: Not available.

supplementation (Xu et al., 2018b; Zhang et al., 2013). However, ammonia inhibition (TAN: 1500–3000 mg N L^{-1}) caused by free ammonia nitrogen (FAN) (>700 mg N L^{-1}) is one of the major concerns for co-digestion with these waste streams (Wang et al., 2014; Zhang et al., 2013). Therefore, it is important to select suitable co-substrate combinations and control the ratio based on FAN and VFA

Table 3
Studies on co-digestion of lignocellulosic biomass.

Co-feedstock	Mixing ratio	Pretreatment	Conditions	C/N ratio	OLR (kg VS m^{-3} d^{-1})	SRT (days)	SMY (mL g^{-1} VS_{added})	$VS_{reduction}$ (%)	Remarks	Reference
Cassava pulp: Swine manure	77:23 (w/w)	No pretreatment	Semi-continuous Mesophilic	35	6	23	380	82	Low cyanide accumulation (0.5 mg L^{-1})	Glanpracha & Annachhatre, 2016
Cassava pulp: Swine manure	3:2 (VS)	No pretreatment	Semi-continuous Mesophilic	33	3.5	15	306	61	Co-digestion resulted in 159% higher SMY compared to mono-digestion of cassava pulp	Panichnumsin et al., 2010
Wheat straw: Microalgal biomass	1:1 (VS)	Thermo-alkaline pretreatment (10% CaO at 72 °C for 24 h)	CSTR Mesophilic	13	1	20	240	48	15% higher SMY with pretreatment compared to that without pretreatment VFA < LOD	Solé-Bundó et al., 2017
Vinasse: Sugarcane press mud cake	73:27 (VS)	No pretreatment	Semi-continuous Mesophilic	NA	2.2	24	366	NA	pH: 7.4; VFA/ALK: 0.2 Co-digestion led to 174% improvement in SMY compared to mono-digestion of sugarcane press mud cake	López González et al., 2017
Liquid hydrolysate of wheat straw: Seaweed hydrolysate	1:1 (COD)	Acid-catalyzed steam pretreatment followed by enzymatic hydrolysis of wheat straw	UASB Mesophilic	NA	6.6 (kg COD m^{-3})	~ 3	220 (mL g^{-1} COD)	96 ($COD_{reduction}$)	pH (~6.9) TAN: (0.1 g N L^{-1})	Nkemka & Murto, 2013
Sugarcane filter cake: Bagasse	7:3 (w/w)	No pretreatment	CSTR Mesophilic	41	3	28	176	NA	Co-digestion resulted in 31% decrease in SMY compared to mono-digestion of filter cake	Janke et al., 2016

C/N: Carbon-to-nitrogen; LOD: Limit of detection; CSTR: Continuous-stirred tank reactor; OLR: Organic loading rate; SRT: Solids retention time, which equals the hydraulic retention time for most anaerobic digesters; SMY: Specific methane yield; VS: Volatile solids; COD: Chemical oxygen demand; VFA: Volatile fatty acid; ALK: Alkalinity; TAN: Total ammonia nitrogen; UASB: Upflow anaerobic sludge blanket; NA: Not available.

accumulation for effective digestion.

3.2. Lignocellulosic feedstocks

Lignocellulosic biomass feedstocks (e.g., agricultural and forestry residues, energy crops, etc.) have great potential in AD due to their high abundance, low cost, and year-round availability (Sawatdeenarunat et al., 2016). However, the slow rate of hydrolysis limits mono-digestion of these highly recalcitrant feedstocks, which is addressed by utilizing often costly pretreatments (Shrestha et al., 2017; Surendra et al., 2015). Thus, co-digestion could reduce both operating costs and chemical usage (Mata-Alvarez et al., 2014; Shrestha et al., 2017). The process stability and SMY of co-digestion of lignocellulosic feedstocks with various co-feedstocks under different working conditions are summarized in Table 3.

The C/N ratio plays a pivotal role in selecting an optimal mixing ratio of lignocellulosic feedstocks with other co-feedstocks. Janke et al. (2016) reported a 39% decrease in SMY during co-digestion of sugarcane filter cake and bagasse compared to mono-digestion of sugarcane filter cake due to recalcitrant component derived from bagasse and high C/N ratio of 41. Furthermore, co-digestion of pretreated wheat straw and microalgal biomass at a ratio of 1:1 (VS basis) enhanced SMY by only 15% compared to co-digestion without pretreatment (Solé-Bundó et al., 2017). This suggests that co-digestion by itself could enhance the digestibility of lignocellulosic feedstocks.

3.3. Sewage sludge

Co-digestion of sewage sludge with rapidly biodegradable feedstocks with higher C/N ratio resulted in improved SMY, provided supplemental alkalinity and trace elements, and diluted heavy metals and pathogens present in sewage sludge (Mehariya et al., 2018; Mata-Alvarez et al., 2014). Bolzonella et al. (2006a) observed a two-fold increase in SMY when sewage sludge was co-digested with the organic fraction of municipal solid wastes (OFMSW) compared with mono-digestion of sewage sludge. However, feedstock availability and handling, process monitoring, and digestate-disposal safety standards are still some of the major challenges in co-digestion of sewage sludge with OFMSW or food waste (Nghiem et al., 2017; Tyagi et al., 2018).

Fat, oil, and grease (FOG) waste co-feedstocks provide a high energy source because lipids have the highest biomethane potential (BMP) (900–1000 mL g^{-1} VS_{added}) compared to carbohydrate (415 mL g^{-1} VS_{added}) and protein (496 mL g^{-1} VS_{added}) (Elalami et al., 2019). Sewage sludge co-digestion with grease trap sludge at the ratio of 7:3 (VS basis) was reported to improve SMY compared to mono-digestion (Table 4) (Davidsson et al., 2008; Grosser et al., 2017; Luostarinen et al., 2009). However, long-chain fatty acids (LCFAs) accumulation and foaming are major concerns of FOG co-feedstocks. Furthermore, co-digestion of sewage sludge with microalgae is beneficial for nutrient recovery due to rapid growth, availability, and low lignin content of algal biomass (Ajeej et al., 2015; Mata-Alvarez et al., 2014). However, a low C/N ratio due to high protein, and pH over 8.5 can inhibit methanogens due to ammonia accumulation (Ajeej et al., 2015). Hence, digester stability could be an issue when using microalgae as a co-feedstock.

3.4. Animal manure

Most co-digestion studies have focused on cattle, swine, and poultry manure as the major animal manure sources. Because of the lower C/N ratio (7.2–7.7), mono-digestion of animal manure often leads to ammonia toxicity and subsequent process instability (Zahan et al., 2018). One of the most effective methods to prevent such toxicity is co-digestion with carbon-rich feedstocks (Li et al., 2018a; Ning et al., 2019). The major benefits of using animal manure as a co-substrate are its high buffering capacity against potential accumulation of VFA and continuous supplementation with relevant microbial populations (Luo et al., 2018). Most long-term studies of co-digestion of agricultural residues use animal manure as the primary feedstock because the availability of agricultural residues varies seasonally (Yue et al., 2013; Zahan et al., 2018).

The SMYs ranged between 258 and 420 mL g^{-1} VS_{added} for cattle manure, about 350 mL g^{-1} VS_{added} for poultry manure, and 281–373 mL g^{-1} VS_{added} for swine manure co-digestion with various co-feedstocks, at a C/N ratio of 13 to 25 (Table 5). Zahan et al. (2018) reported that the

Table 4
Studies on co-digestion of sewage sludge.

Co-feedstock	Mixing ratio	Conditions	OLR (kg VS m^{-3} d^{-1})	SRT (days)	SMY (mL g^{-1} VS_{added})	$VS_{reduction}$ (%)	Remarks	Reference
Sewage sludge: Grease trap sludge	7:3 (VS)	Pilot-scale	2.5	10	344	58	About 27% increase in SMY and VS reduction in co-digestion than mono-digestion of sewage sludge	Davidsson et al., 2008
Sewage sludge: Grease trap waste	7:3 (VS)	Lab-scale	3.5	16	463	67	About 67% higher SMY in co-digestion than mono-digestion of sewage sludge	Luostarinen et al., 2009
Sewage sludge: Grease trap waste	22:3 (VS)	Lab-scale	1.9	10	349	50	About 93% higher SMY in co-digestion than mono-digestion of sewage sludge	Grosser and Neczaj, 2016
Sewage sludge: Grease trap waste: OFMSW	4:3:3 (VS)	Lab-scale	~1.8–2.2	NA	547	80	Co-digestion led to 20% higher SMY than mono-digestion of sewage sludge	Grosser et al., 2017
Sewage sludge: OFMSW	4:1 (VS)	Full-scale	~0.8–1.0	20	~600–890 (biogas yield)	81	Electrical energy and heat production increased by 130% and 55% respectively during co-digestion compared to mono-digestion of sewage sludge	Zupančič et al., 2008
Sewage sludge: OFMSW	21.4 (VS)	Full-scale	1.2	19.8	171	NA	Lower TKN and total P in food waste than sewage sludge 20% increase in SMY compared to mono-digestion of sewage sludge	Bolzonella et al., 2006a
Secondary sludge: OFMSW	3:2 (VS)	Full-scale	0.8	35.6	275	NA	Higher TKN and total P in co-digestate 3-fold increase in SMY during co-digestion compared to mono-digestion of secondary sludge	Bolzonella et al., 2006b

All the studies were conducted in continuous-stirred tank reactor at mesophilic condition. C/N: Carbon-to-nitrogen; OLR: Organic loading rate; SRT: Solids retention time, which equals the hydraulic retention time for most anaerobic digesters; SMY: Specific methane yield; VS: Volatile solids; OFMSW: Organic fraction of municipal solid waste; TKN: Total Kjeldahl nitrogen; NA: Not available.

Table 5
Studies on co-digestion of animal manure.

Co-feedstock	Mixing ratio	Conditions	C/N ratio	OLR (kg VS m^{-3} d^{-1})	SRT (days)	SMY (mL g^{-1} VS_{added})	$VS_{reduction}$ (%)	Remarks	Reference
Dairy manure: Meat and bone meal: Crude glycerol	1:0.7:0.3 (VS)	Semi-continuous	13	2.7	30	420	47	About 2-fold increase in NH_4^+-N during co-digestion compared to mono-digestion of dairy manure	Andriamanohiarisoamanana et al., 2018
Chicken manure: Food waste: Wheat straw	3:1:1 (NA)	Semi-continuous	21.9	2.0 (kg TS m^{-3} d^{-1})	20	351	42	Co-digestion resulted in 93.4% higher SMY compared to mono-digestion of chicken manure	Zahan et al., 2018
Cattle manure: Cheese whey	1:1 (v/v)	Two-phase	NA	1.7 (kg COD m^{-3} d^{-1})	20	258	83 (sCOD)	Two-phase resulted in 2-fold increase in methane yield compared to that from one-phase process	Bertin et al., 2013
Swine manure: Olive mill wastewater	3:2 (NA)	CSTR	NA	4.4	30	373	71	No negative impact on SMY despite increase in inhibitory compounds (phenols)	Kougias et al., 2014
Chicken manure: Apple pulp	2:1 (NA)	Semi-continuous	18.5	4.8	25	340	NA	No inhibition caused by VFA and TAN accumulation in co-digestion compared to mono-digestion of chicken manure	Li et al., 2018a
Swine manure: Corn stover (pretreated at 5% NaOH)	1.2:1 (NA)	CSTR	25	2.0	~21	282	NA	Enhanced methane production compared to mono-digestion of swine manure	Ning et al., 2019

All the studies were conducted at lab-scale under mesophilic condition. C/N: Carbon-to-nitrogen; OLR: Organic loading rate; SRT: Solids retention time, which equals the hydraulic retention time for most anaerobic digesters; SMY: Specific methane yield; VS: Volatile solids; TS: Total solids; COD: Chemical oxygen demand; sCOD: Soluble chemical oxygen demand; VFA: Volatile fatty acid; TAN: Total ammonia nitrogen; CSTR: Continuous stirred-tank reactor; NA: Not available.

combination of two feedstocks involving animal manure yielded higher biogas than a combination of three or more feedstocks at low OLR. However, at high OLR, a combination of three or more feedstocks helped to achieve a better C/N ratio balance. This suggests that the effect of C/N ratio is more pronounced at higher OLRs. Furthermore, higher proportions of animal manure in the co-substrate mixture can counter the accumulation of VFA and maintain desirable nutrients and moisture balance (Xavier et al., 2015).

4. Microbial communities in anaerobic co-digestion

The AD microbial community is one of the most important drivers of the anaerobic bioconversion of diverse feedstocks in AD processes. Compared to mono-digestion, co-digestion systems tend to support microbial communities with higher diversity as diverse microorganisms are continuously introduced through co-feedstocks.

Most bacteria in conventional AD are grouped into *Firmicutes*, *Chloroflexi*, *Bacteroidetes*, *Proteobacteria*, and *Actinobacteria* (Dai et al., 2016; Zamanzadeh et al., 2017). However, feedstock type plays an important role in microbial community structure. For example, a sewage sludge-fed AD system supported a bacterial community consisting of *Firmicutes* (40.8%), *Bacteroidetes* (23.9%), *Proteobacteria* (5.9%), and *Chloroflexi* (1.1%), whereas a similarly operated manure-fed reactor harbored a community consisting of *Chloroflexi* (52.9%), *Firmicutes* (20.6%), *Bacteroidetes* (6.6%), and *Proteobacteria* (6.3%) (Dai et al., 2016). In the same study, the co-digestion of sewage sludge and cattle manure at the ratio of 3:7 (VS basis) and pH of 9.0 resulted in a higher relative abundance of *Firmicutes* (57.4%) than mono-digestion reactors fed with either feedstock.

The ratio of the different feedstocks and their biodegradability also impact the microbial community structure. For example, Fitamo et al. (2017) reported a higher ratio of slowly degradable feedstock in the co-feedstock mixture resulted in lower microbial community diversity. Moreover, a semi-continuous co-digestion study using chicken manure and apple pulp at a ratio of 2:1 (VS basis) was found to better withstand VFA and TAN at high OLR due to greater levels of *Methanobacteriales* (0.17×10^9 cells mL^{-1}) and *Methanosarcinales* (0.67×10^9 cells mL^{-1}) compared to mono-digestion of chicken manure (Li et al., 2018a). Several co-digestion studies reported that the accumulation of inhibitory compounds resulted in an increased archaeal diversity and a shift from acetoclastic to hydrogenotrophic methanogenesis both in batch and continuous reactors (Farhat et al., 2018; Li et al., 2018a, 2018c; Zamanzadeh et al., 2017). These studies suggest that hydrogenotrophic methanogens are more tolerant to operational disturbances compared to acetoclastic methanogens. However, full-scale studies are needed to corroborate these findings.

It is important to point out that microbial diversity is not the only factor that should be considered when evaluating the efficiency of AD processes; the functional capacity and resilience of the community are equally important. It is widely accepted that co-feedstocks improve the stability and overall digestibility via a better balance of nutrients and trace elements that facilitate enzymatic activities (Guilford et al., 2019; Xu et al., 2018b). The enzymes involved in hydrogenotrophic methanogenesis and syntrophic acetate oxidation require trace elements such as Se, Mo, W, Co, Ni, Zn, and Fe (Xu et al., 2018b). High concentrations of Zn are present in animal manure, most likely contributed by growth-promoting feed additives (Rayne and Aula, 2020), making it a good candidate as a co-feedstock.

Further research is needed to identify the mechanisms responsible for the accumulation of inhibitory compounds under different operating conditions with a particular focus on linking the microbial community structure and function to AD operating conditions for better process optimization. Meta-omics (Herold et al., 2020) and stable isotope probing (Ziels et al., 2018) methods will be useful in such studies.

5. Kinetic modeling of co-digestion

Methane or biogas production kinetics can be used to evaluate the biodegradability patterns of organic matter during AD. Various conventional mono-digestion models such as first-order, logistic, modified Gompertz, cone, transfer, etc., have been tested to examine the kinetics of co-digestion in batch studies (Panigrahi et al., 2020; Pan et al., 2019). Parameters such as rate constant (first-order), lag phase (modified Gompertz), or shape factor (cone) are used to compare the activity, adaptability, and compatibility of inocula with various co-feedstock ratios. However, the best fit model may not contain all the necessary indicators to explain the kinetics such as the rate constant (k) (not included in modified Gompertz model) and lag-phase (λ) (not included in the cone model).

Typically, biogas production during co-digestion of complex organics and pretreated feedstocks exhibits two peaks. The readily biodegradable fraction of the combined feedstock is responsible for a first peak in the biogas production curve, whereas the second peak is characteristic of the slowly biodegradable portion (Masih-Das and Tao, 2018; Pan et al., 2019). Models have been developed specifically to describe this two-peak phenomenon since the conventional mono-digestion models only describe single-stage cumulative methane yields (Adarme et al., 2019; Masih-Das and Tao, 2018; Mendieta et al., 2020; Pan et al., 2019).

The superimposed model (the modified Gompertz model coupled with the first-order kinetic model) describes a two-peak methane production during co-digestion. For example, the superimposed model showed the best fit of two-peaks ($R^2 > 0.999$) for the co-digestion of pig manure and food waste at a ratio of 1:1 (VS basis), compared to the first-order and modified Gompertz models (Wang et al., 2020). The modified Gompertz model was also combined with the second-order equation to model two-peak biogas production, which showed a better fit ($R^2 =$ 0.993–0.998) for food waste and liquid dairy manure co-digestion compared to the modified Gompertz model alone (Masih-Das and Tao, 2018).

Some studies also used the terminologies “two-substrate model” or “two-phase exponential model” which describe the same two-stage phenomenon that separates the rate constant into two-equation terms (e.g., rapid and slow rate constants) (Adarme et al., 2019; Pan et al., 2019). This model better described the methane production from sugarcane biorefinery by-products co-digestion based on the values of error functions, such as R^2, Akaike’s Information Criterion, compared to the modified Gompertz model (Adarme et al., 2019). However, the two-phase exponential model was the least fitting and precise, based on the values of error functions, compared to the modified Gompertz model and cone model for sewage sludge and food waste co-digestion (Pan et al., 2019).

Further development of new models to fit the cumulative SMY with two kinetic constants and a lag phase is essential to facilitate progress with the understanding of two-peak or two-stage anaerobic degradation due to different feedstock combinations. Also, the application of more complex modeling such as Anaerobic Digestion Model No. 1 (ADM1) based on a two-stage kinetic model needs to be examined.

6. Digestate management

6.1. Digestate dewaterability

The total solids (TS) content of the digestate is an important factor to consider when evaluating transportation costs for land applications. The dewaterability of digestate relies heavily on its characteristics such as VS content, extracellular polymeric substances, and soluble microbial products (Nghiem et al., 2017). It has been reported that co-digestion can also modify digestate dewaterability. In a study by Leiva et al. (2014) using thickened waste activated sludge from a wastewater treatment plant fed with fruit juice/winery wastewater as a co-substrate, enhanced the dewaterability and reduced the pathogen density compared to mono-digestion of municipal sludge cake. In addition, another study found that decreasing the retention time in the co-digestion of pig manure and food waste also significantly improved the dewaterability (Dennehy et al., 2018).

6.2. Direct application of digestate

Co-digestion can result in higher potential use of digestate as a soil amendment due to two main factors - total nutrient levels and nutrient bioavailability. Recent studies focused on direct application of co-digestate without any mechanical separation based on its nutrient content (Wang et al., 2019), agricultural yields (Elalami et al., 2020a, 2020b; Iocoli et al., 2019; Solé-Bundó et al., 2017), and phytotoxicity factors (Bres et al., 2018; Elalami et al., 2020a, 2020b; Solé-Bundó et al., 2017).

Total nutrient content or fertility (summation of total N, total P, and total K) of 7.4% (w/w) of a corn slag waste and dairy manure co-digestion was higher than mono-digestion of the individual feedstocks (Wang et al., 2019). Furthermore, higher nutrient availability (NH_3, TKN, and total P) due to co-digestion of macroalgae residue with sewage sludge resulted in higher wheat growth (approximately 62.5%, dry weight basis), compared with macroalgae mono-digestion (Elalami et al., 2020a). Relative to microalgae digestate alone, about 45.5% increase in the growth index of *Lepidium sativum* (L.) was also observed in microalgae and sewage sludge co-digestate, diluted at 0.1% (v/v) before application (Solé-Bundó et al., 2017). Similarly, the co-digestate of cattle manure and onion residue resulted in a 47.8% higher coverage area of *Lactuca sativa* (L.) compared to cattle manure digestate alone (Iocoli et al., 2019). Contrary to this, the digestate derived from sewage sludge mono-digestion and co-digestion with macroalgal residues resulted in a similar dry weight of *Solanum lycopersicum* (L.) (Elalami et al., 2020a, 2020b), which could be due to different nutrient requirements of this particular plant species.

Excessive dosage or continued application of digestate can result in phytotoxicity (i.e., increase in salinity and inhibition of plant growth) (Alburquerque et al., 2012; Bres et al., 2018). The EC_{50} (half-maximal effective concentration; % v/v) of *Daphnia magna* immobilization test was reported to be 2.6% in co-digestate from poultry manure and vegetable waste co-digestion compared to mono-digestate from poultry manure (1.8%) (Bres et al., 2018). The lower phytotoxicity of co-digestate, corresponding to a higher germination index, was observed at high concentration of co-digestate (diluted at 10% v/v) (Solé-Bundó et al., 2017). On the other hand, there was no significant difference at lower concentrations (1% and 0.1% v/v), which suggests that the digestate concentration influences the phytotoxicity.

6.3. Liquid fraction of digestate

The liquid fraction of digestate (LFD) from swine manure, food waste, and maize silage co-digestate can substitute synthetic N fertilizer based on maize yield with better ecological benefits, especially in the soil (Sigurnjak et al., 2017). LFD can also be diluted and used as a medium for micro- and macro-algae production as it is high in nutrients and low in suspended solids. Nutrient-rich LFD can further be used for vegetable/fruit production via bioponics (Wongkiew et al., 2021). The application of LFD from co-digestion of olive waste and citrus pulp with animal manure showed improvement in soil fertility in terms of both soil chemistry (organic matter and water-soluble phenol) and bioconversion (microbial biomass, catalase, and fluorescein diacetate hydrolysis) (Muscolo et al., 2017). Co-digestion of dairy manure with meat and bone meal and crude glycerol resulted in 2.1 to 2.3-fold increase in NH_3-N due to higher organic N in meat and bone meal compared to mono-digestion of dairy manure (Andriamanohiarisoamanana et al., 2018).

6.4. Solid fraction of digestate

Mono-digestate from Ca-rich feedstocks resulted in an increased amount of amorphous Ca-P; thus limiting P availability to plants (Grigatti et al., 2015). Furthermore, mono-digestate from agricultural residues had a higher humification index due to the presence of recalcitrant organic matter (Kataki et al., 2017). Therefore, feedstocks should be co-digested for nutrient balance and reduced phytotoxicity. The solid fraction of co-digestate can be subjected to composting or co-composting for improved digestate quality (Damaceno et al., 2019). Composting of co-digestate from cattle slurry and silage, with or without vine shoot pruning as co-compost, resulted in suppression of plant pathogen *Fusarium oxysporum* f. sp. *melonis* (Bustamante et al., 2012). It was further suggested that co-composting the co-digestate with bulking agents such as vine shoot pruning reduces temperature and electrical conductivity and dilutes heavy metal concentration in the end-products (Bustamante et al., 2012). Moreover, stabilization via vermicomposting also increased the concentration of the plant-growth regulator kinetin (Rékási et al., 2019).

The mono-digestate derived from feedstocks such as food waste suppressed mycelium colonization and mushroom yield due to high salt content, ensuing an elevated conductivity (Sánchez, 2010). However, the mushroom (*Pleurotus ostreatus)* yield was increased when grown on wheat straw and millet supplemented with solid co-digestate (derived from broiler chicken litter and wood chip bedding co-digestion) compared to feedstocks supplemented without co-digestate (Isikhuemhen and Mikiashvilli, 2009). Furthermore, mushroom cultivation also produces residual spent mushroom feedstock, which can then be used as a feedstock in co-digestion or as a valuable soil amendment (Luo et al., 2018).

BSF farming on diverse feedstocks produces nutrient-rich animal feed, organic fertilizer, and other biobased products (Surendra et al., 2020). Co-digestate from pretreated rapeseed straw and chicken manure (1:3; VS basis) resulted in a higher fatty acid methyl esters recovery, showing a yield of 301.8 mg g^{-1} dry weight (Elsayed et al., 2020) during BSF rearing. Moreover, co-digestate could be suitable for BSF farming due to the suppression of pathogens such as *Salmonella* spp., *Escherichia coli,* and *Bacillus* spp. (Jiang et al., 2020, 2019, 2018), and a reduction in heavy metals accumulation as commonly observed in mono-digestate (Chen et al., 2014). Further research on the use of co-digestate for BSF farming needs to be conducted with respect to food safety concerns.

Co-digestate-derived biochar via feedstocks such as cattle manure and grass silage performed better as a slow-release fertilizer than that of raw feedstocks (Pituello et al., 2015) as co-digestion resulted in an increase in the macronutrients (N and P) (Damaceno et al., 2019; Xie et al., 2018). The adsorption capacity of biochar depends on its porosity and surface chemical properties, which are mainly governed by feedstock type and pyrolysis conditions (Pituello et al., 2015). Further research is needed to compare biochar quality between mono- and co- digestates.

7. Challenges and perspectives

Co-digestion has great potential to improve the digestibility of diverse feedstocks for waste management and bioenergy and other high-value product generation. However, co-digestion still entails operational risks associated with its year-round feedstock availability, feedstock complexities due to different biodegradability rates, and co-digestate safety concerns for agricultural applications, especially when feedstocks such as sewage sludge and animal manure are used. Furthermore, it is challenging to determine an optimal ratio for different feedstocks, as the optimal combination of feedstocks is affected by various factors such as feedstock type, composition, trace elements content, and biodegradability, among others.

To address the abovementioned challenges, characterization of the chemical composition of different feedstocks needs to be carried out to assess an optimal mixing ratio. Furthermore, technoeconomic analysis and life cycle assessment are crucial in co-digestion studies, based on feedstock type, the associated feedstock production costs and logistics, which would help to propose the best-case scenario for potential co-digestion biorefineries.

More in-depth analyses focused on microbial communities also need to be conducted to study the effect of co-feedstocks on process efficiency. It is essential to correlate feedstock types and microbial community structure and function. In addition, modifications to the existing kinetic model or developing a standard model for co-digestion can help facilitate process scale-up.

8. Conclusions

Anaerobic co-digestion is a promising strategy for effective waste management and resource recovery, while promoting economic and environmental sustainability. However, further research should focus on developing new approaches to characterize the complex feedstocks and quantify different hydrolysis rates, improving mathematical models to better predict the multitude of interactions, and studying the dynamics of the microbial community and the associated pathways in substrate degradation.

CRediT authorship contribution statement

Renisha Karki: Investigation, Visualization, Formal analysis, Writing - original draft. **Wachiranon Chuenchart:** Visualization, Investigation, Formal analysis, Writing - original draft. **K.C. Surendra:** Writing - review & editing. **Shilva Shrestha:** Writing - review & editing. **Lutgarde Raskin:** Writing - review & editing. **Shihwu Sung:** Writing - review & editing. **Andrew Hashimoto:** Writing - review & editing. **Samir Kumar Khanal:** Supervision, Conceptualization, Writing - review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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