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Review Article

Dietary mitigation of enteric methane emissions from ruminants: A review of plant tannin mitigation options☆

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ABSTRACT

Methane gas from livestock production activities is a significant source of greenhouse gas (GHG) emissions which have been shown to influence climate change. New technologies offer a potential to manipulate the rumen biome through genetic selection reducing CH_4 production. Methane production may also be mitigated to varying degrees by various dietary intervention strategies. Strategies to reduce GHG emissions need to be developed which increase ruminant production efficiency whereas reducing production of CH_4 from cattle, sheep, and goats. Methane emissions may be efficiently mitigated by manipulation of natural ruminal microbiota with various dietary interventions and animal production efficiency improved. Although some CH_4 abatement strategies have shown efficacy in vivo, more research is required to make any of these approaches pertinent to modern animal production systems. The objective of this review is to explain how anti-methanogenic compounds (e.g., plant tannins) affect ruminal microbiota, reduce CH_4 emission, and the effects on host responses. Thus, this review provides information relevant to understanding the impact of tannins on methanogenesis, which may provide a cost-effective means to reduce enteric CH_4 production and the influence of ruminant animals on global GHG emissions.

1. Introduction

Minimizing enteric methane emission from ruminant production whereas enhancing feed conversion efficiency (FCE) and dietary nutrient utilization is a goal for sustainable livestock production. Numerous studies of greenhouse gas (GHG) mitigation strategies by genetic, dietary feed additives, plant extracts and chemical supplementation have been conducted to assess their potential to reduce methanogenesis (Nagaraja et al., 1997; Beauchemin et al., 2008; Hristov et al., 2013a, b; Gerber et al., 2013; Waghorn and Hegarty, 2011). However, most proposed mitigation strategies have shown inconsistent results among studies and may even lead to increased GHG emissions and adverse effects on aspects of animal growth and performance.

Many researchers have reported the effects of plant secondary compounds, such as tannins, saponin and essential oils, as alternative feed additives to modify ruminal fermentation, antimicrobial activity, astringency to deter consumption, to improve animal productivity and mitigate CH_4 production. This review is aimed at providing information on the influence of plant tannins on ruminal microbiota, CH_4 production and animals' performance. Tannins are natural polyphenolic biomolecules that can be found in the bark, wood, fruit, leaves, flowers, and roots of most plant species. Plant tannins may play a role in mitigating methanogenesis. Several studies have evaluated the relationship between tannin-rich diets and CH_4 production in ruminants both in vivo and in vitro

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(Beauchemin et al., 2007; Jayanegara et al., 2010, 2012; Goel and Makkar, 2012; Min and Solaiman, 2018). In vitro studies have shown that tannins have anti-methanogenic activity, either directly by inhibiting methanogens or indirectly by targeting protozoa (Bhatta et al., 2009; Jayanegara et al., 2015). A meta-analysis by Jayanegara et al. (2012) showed that tannin-containing diets or tannin extracts usually reduce enteric CH_4 production. In addition, the effects on animal production and efficiency of animal production need to be evaluated. Methods and practices to reduce CH_4 emissions need to be evaluated in terms of effects on dry matter intake (DMI), microbial activities, and rumen fermentation efficiency (e.g., acetate-to-propionate ratio [A:P]; Goel et al., 2009).

Feed consumed by cattle and other ruminants is fermented by microbes naturally present in the rumen. Fermentation of carbohydrates into volatile fatty acids (VFA), and microbial protein synthesis, are accompanied by the release of gases such as carbon dioxide (CO_2) and CH_4 (Johnson and Johnson, 1995; Gerber et al., 2013). Limited studies have considered the relationship between plant tannins and CH_4 emissions per unit of DMI, animal performance, rumen fermentation, and feed efficiency dynamics (Waghorn and Hegarty, 2011; Beauchemin et al., 2007). This review summarized available literature on the impact of DMI and tannins on GHG emissions, rumen fermentation, and animal growth performance associated with rumen microbial activities in different ruminant species. Opportunities for reducing rumen methanogenesis through dietary inclusion of tannins are also discussed.

2. Global challenges of livestock industry

In 2015, there were 7.5 billion peoples in the world, and the World Hunger Map estimated that 795 million of those individuals did not have an adequate food supply (WFP, 2015). Meanwhile, published models forecast the world's human population to reach 9.7 and 11.2 billion in 2050 and 2100, respectively (UN, 2015). To meet food demands for this increasing population, it was estimated that milk and meat production must increase by 63% to 76%, respectively (Alexandratos and Bruinsma, 2012). As countries move from developing to developed, there tends to be an increase in per capita protein consumption as well that should be considered in the forecast. In addition, global demand for livestock products is expected to double by 2050 (Rojas-Downing et al., 2015). Increasing food production will likely result in an increase in GHG emissions, including enteric CH_4 from animals, manure, crop production (i.e., anaerobic fermentation in rice production system), and cropland with inorganic or organic fertilization, unless mitigation practices are discovered and implemented. On a global scale, it has been estimated that livestock production contributes up to 10% of total GHG emissions; however, that value does not included indirect costs associated with agricultural activities, such as fossil fuels combustion and chemical fertilizers (IPCC et al., 2013; Gerber et al., 2013).

3. Methanogenesis

Methane gas is formed by anaerobic archaea coupled with bacteria, protozoa, and fungi in the rumen ecosystem. Up to 28 genera and 113 species of methanogens are known to exist in nature (Janssen and Kirs, 2008), and 5 of these species belong to *Methanobrevibacter* and *Methanosarcina* genera. Both *Methanobrevibacter ruminantium* and *Methanomicrobium mobile* was considered the dominant methanogen in the rumen (Yanagita et al., 2000; Whitford et al., 2001; Hristov et al., 2012; Min et al., 2014a, b). Whereas Janssen and Kirs (2008) reported that *Methanobrevibacter* was the dominant methanogen in the rumen (61.6%), other studies have shown that there is a diversity of methanogens. In addition, CH_4 production also varies with animal species, DMI, type of forage fed, concentrate-to-forage ratio, efficiency of feed conversion, plant secondary metabolites, and rumen fermentation characteristic, e.g., VFA, hydrogen (H_2) etc (Tajima et al., 2001; Wright et al., 2006, 2009; Wadhwa et al., 2016). A large population of methanogens exists in the rumen; however, there has been no straight-forward consensus on the association between the total population of methanogens and the magnitude of CH_4 emissions (McSweeney and Mackie, 2012). A summary of methanogenesis and microbial fermentation of dietary components in the rumen resulting in the production of VFA, CH_4, CO_2, and H_2 emitted through eructation is presented in Fig. 1.

It has been noted that feeding grain-based diet that are high in starch instantly lowered CH_4 emission (g/d and g/kg DMI); whereas, diets with forage-based diet resulted in increased CH_4 emissions (Fig. 1; Wallace et al., 2014). In ruminants, 87% to 89% of enteric CH_4 production is from the rumen, 11% to 13% is produced in the hindgut of gastrointestinal tract (Murray et al., 1976, 1978; Lassey et al., 1997). The general biological reactions have been described by Van Soest (1994) as follows: Glucose ($C_6H_{12}O_6$) + ammonia (NH_3) → Rumen microbes + CH_4 + CO_2 + VFA. Thus, ruminants require glucose and nitrogen (N) to ensure sufficient microbial protein and VFA synthesis to meet animal requirements for growth, maintenance, and production. Multiple possible pathways of glucose fermentation result in different quantities of H_2 formed; therefore, quantity of CH_4 produced from glucose varies depending on microbial activity and biological reactions (Janssen, 2010). In the rumen, methanogens use H_2 to reduce CO_2 to CH_4 (Van Soest, 1994). In this pathway, which may involve coenzyme M (Miller et al., 1986), 4 mol of H_2 are used to produce CH_4 (Czerkawski, 1986). Formation of butyrate + H_2 or acetate + butyrate + H_2 have been shown to be predominant pathways under low ruminal H_2 concentrations, whereas the accumulation of acetate + propionate was predominant at higher H_2 concentrations (Janssen, 2010). If ruminal VFA production favors less acetate production relative to propionate (i.e., lower A:P ratio), the net equilibrium of H_2 in the rumen decreases and results in reduced CH_4 formation (van Nevel and Demeyer, 1996). Most rumen methanogens attain energy for their growth through a sequence of biological reduction of CO_2 with H_2 (methanogenesis pathway; $4H_2 + CO_2 \rightarrow CH_4 + 2H_2O$), whereas some methanogens use the acetogenesis pathway ($CH_3COOH \rightarrow CH_4 + CO_2$) (Liu and Whitman, 2008; Attwood and McSweeney, 2008). In-depth reviews of ruminal methanogenesis were provided by Ungerfeld et al. (2015, 2018) and Nakamura et al. (2010). Alternative strategies to reduce CH_4 emissions in ruminants, which are discussed in the following section, may reduce enteric GHG production and simultaneously improve FCE and profitability.

4. Methane measurement methods

Emissions of CH_4 from ruminants are highly variable between animal species and detection methods (Table 1). Various methods to record CH_4 emissions from individual animals have been established, each with their own advantages, disadvantages, and scope of application. The most widely used techniques are the indirect respiration chambers (IRC), the sulfur hexafluoride tracer technique (SF_6), the automated head-chamber system (GreenFeed system [GF]; C-Lock Inc., Rapid City, SD, USA), and laser CH_4 detectors (LMD; Laser Methane Mini, Tokyo Gas Engineering Solutions, Ltd., Tokyo, Japan). Studies that compared techniques have reported inconsistent results (Hristov et al., 2017). The standard method against which other methods are benchmarked is the IRC. However, IRC are costly and labor intensive, proving prohibitive to obtain measurements on large numbers of animals. Furthermore, individual confinement within the IRC imposes restrictions of the feeding and natural behavior of the animals under study. Recently, alternative GF methods have been developed (Zimmerman and Zimmerman, 2012). The GF system is a

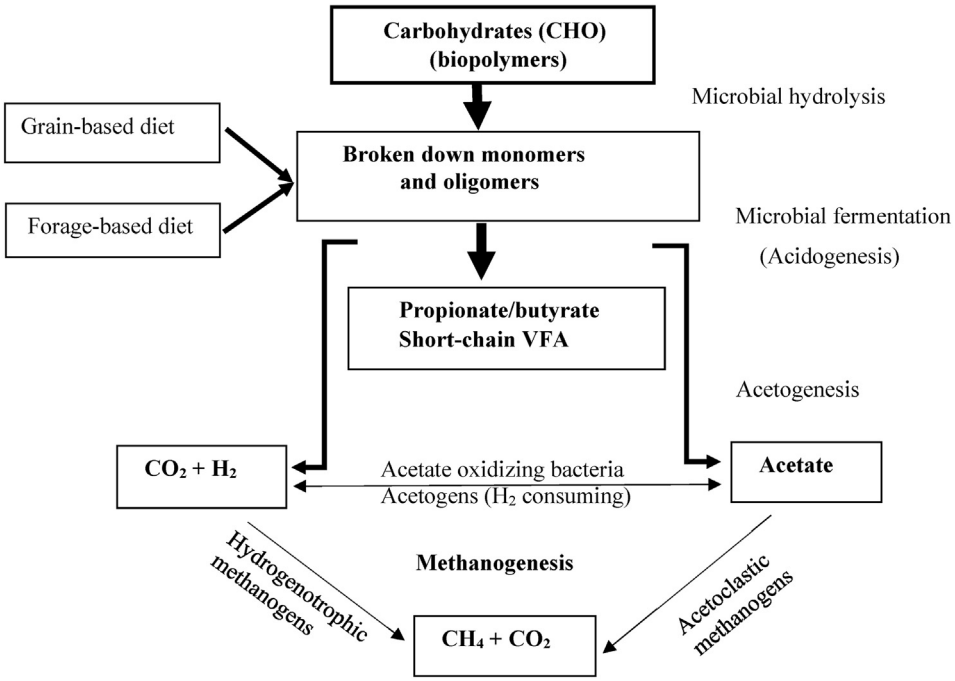


Fig. 1. Schematic microbial fermentation of polysaccharides, acetogenesis, and methanogenesis in the rumen. VFA = volatile fatty acids. Boxes with bold solid lines are potential targets for suppressing CH_4 emissions. Sources: Attwood and McSweeney (2008), Beauchemin et al. (2008), Morgavi et al. (2010), Patra (2012, 2016).

mass flux measurement system with clustering of animals visiting the GF at specific times, depending on the unit type and housing conditions. The instrument's mode of action is to measure emissions directly from animals by delivering a small feed treat. The animals are assigned with an instrument-recognizable identifier and emissions are measured when cattle insert their heads into the instrument to consume the delivered feed. Even though this method is less stressful for animals than IRC, the method has some shortcomings. Consideration must be given to the number of animals with access to the GF, and duration of sampling, to avoid bias associated with clustering of animals visiting the GF at specific times (Hammond et al., 2016a,b).

Another extensively used technique to determine enteric CH_4 emissions is the SF_6 tracer method (Zimmerman, 1993). For this method, a bolus containing SF_6 is deposited in the rumen and concentrations of SF_6 and CH_4 in the breath are analyzed by gas chromatography. The concentration of CH_4 is corrected for dilution by external air from the measured SF_6 concentration. Results with the SF_6 technique have been inconsistent (Pinares-Patino and Clark, 2008; Pinares-Patino et al., 2011), but the modifications by Deighton et al. (2014) decreased the most serious sources of error.

Another new measurement method of CH_4 is the LMD, a hand-held open path laser measuring device, namely tunable diode laser absorption spectroscopy. It was originally developed for the detection of gas leaks, and therefore, discriminates between high CH_4 concentrations and the low background concentration in the atmosphere (Crowcon, 2014). However, there was not a strong relationship LMD and the dynamics of CH_4 concentrations exhaled by ruminants (Chagunda, 2013) and dairy wastewater (Todd et al., 2011). When it is used to study the CH_4 emission of animals, an operator points the device a fixed distance from the snout of a cow for a duration of several minutes, once or multiple times a day, and the cumulative CH_4 concentration along the laser path is quantified and recorded in real-time for large groups of animals. A variant of the LMD method is to determine atmospheric CH_4 concentrations down-wind and up-wind of a group of animals grazing a paddock or in large confined areas such as a beef feed yard (Todd et al., 2016). Therefore, it is of great value for researchers to know and understand the extent of variability and comparability among the available measurement methods prior to investing considerable time and instrumentation/labor expense in recording emissions from a large number of animals.

5. Interrelationships between methane production, DMI and FCE

Results from a known set of published experiments examining the effects of CH_4 detection method, cattle type (beef vs. dairy) and DMI were assembled and summarized in Table 1. A simple regression analysis using Proc Reg in SAS (SAS, 2004) was conducted to evaluate the extent to which diets and DMI were related to CH_4 emissions from cattle.

5.1. Dry matter intake and methane emissions

When the regression analysis was conducted using the data in Table 1, CH_4 production was strongly correlated with DMI as described by Eq. (1).

$$CH_4(g/d) = 20.53 \times DMI(kg/d) + 24.62 \left(R^2 = 0.82; P < 0.001\right) \quad \text{Eq. (1)}$$

Each 1.0-kg increase in DMI increased CH_4 production by an average of 20.53 (±0.87) g per kg of DMI in beef and dairy cattle. However, there was not a strong relationship (Fig. 2A) between different CH_4-measurement methods (IRC, SF_6, and GF). The slope of the proposed general relationship between CH_4 and DMI was similar to previously published values which range from 17.0 to 25.0 g/kg DMI (Clark et al., 2005; Grainger et al., 2007; Yan et al., 2009; Dijkstra et al., 2011; Charmley et al., 2016). Our average predicted relationship (CH_4 at 20.53 g/kg DMI) was similar to the 20.7 g/kg DMI found in Australian cattle (Charmley et al., 2016) and by other researchers

Table 1
Selected studies of methane emissions from widely used techniques[1].

Reference	Animal breed	BW, kg/animal	Ration type	DMI[2], kg/d per animal	CH_4[2], g/kg DMI	Technique used
Beef cattle						
Alemu et al. (2017)	heifer	380 to 404	low-RFI	7.4	27.4	GF
			high-RFI	7.9	28.12	GF
			low-RFI	6.0	26.5	IRC
			high-RFI	6.3	26.5	IRC
Beauchemin and McGinn (2005)	steer	328.0	corn-based	6.83	9.2	IRC
			barley-based	6.17	13.1	IRC
Beauchemin and McGinn (2006)	heifer	328.3	high-forage (70%)	6.2	21.35	IRC
			high-grain (56%)	7.5	20.13	IRC
Dini et al. (2019)	steer	536.2	high-RFI	10.6	28.1	SF_6
			low-RFI	9.33	20.3	SF_6
Hales et al. (2015)	steer	223.5	steam-flake corn	5.1	11.65	IRC
			dry-rolled corn	5.3	14.06	IRC
			beef TMR	5.2	12.88	IRC
			beef TMR + WDGS	5.2	12.83	IRC
Hammond et al. (2015)	heifer	317 to 339	grazing			
			period I	7.62	26.6	GF
				7.66	28.3	IRC
			period II	7.6	27.8	GF
				7.54	27.7	IRC
			period III	9.15	18.8	GF
				9.15	21.5	SF_6
			ryegrass	8.28	24.1	GF
				10.0	17.3	GF
				8.13	28.4	IRC
				10.0	21.8	SF_6
			RC	6.86	29.5	GF
				8.69	18.5	GF
				7.10	28.1	IRC
				8.69	23.0	SF_6
			BT	7.93	28.9	GF
				7.51	29.2	IRC
			wild flowers[3]	7.34	28.8	GF
				8.78	19.7	GF
				7.42	25.7	IRC
				8.78	19.5	SF_6
Hammond et al. (2015)	heifer	317 to 339	ryegrass	10.0	21.8	SF_6
			RC	8.69	23.0	SF_6
			wild flowers[3]	8.78	19.5	SF_6
	steer	519	feedlot	7.2	15.0	GF
Herd et al. (2016)			roughage	7.6	19.0	GF
Jonker et al. (2016)	Hereford/Friesian heifer	382	alfalfa silage-based			
			period I	5.9	24.0	IRC
				5.9	22.7	SF_6
				5.9	24.3	GF
			period II	7.5	24.5	IRC
				7.1	22.2	SF_6
				7.2	24.7	GF
			period III	8.3	24.6	IRC
				8.4	22.6	SF_6
				8.3	26.6	GF
			period IV	10.9	24.5	IRC
				12.2	22.4	SF_6
				12.1	26.8	GF
McCaughey et al. (1997)	steer	356.2	rotational stocking			SF_6
			HSR	14.94	17.65	
			LSR	13.61	20.85	
			continuous stocking			
			HSR	13.51	17.92	
			LSR	13.20	23.23	
McGinn et al. (2009)	steer	381.2	barley grains (35%)	9.5	23.8	SF_6
			corn DDGS (35%)	9.0	19.9	
Pedreira et al. (2013)	steer	444.3	with no concentrate, 100% SS	5.52	22.76	SF_6
			30% concentrate + 70% SS	7.9	18,97	
			60% concentrate + 40% SS	8.7	16.13	
Tomkins et al. (2015)	steer	226.8	chopped Rhodes grass	5.4	14.60	IRC
Dairy cattle						
Aguerre et al. (2011)	Holstein	620.7	forage-to-concentrate ratio			IRC
			47:53	18.2	25.9	
			54:46	18.4	28.2	
			61:39	17.6	29.1	
			68:32	17.5	31.9	
Arbre et al. (2016)	dairy cow	723 to 729	60% hay + 40% grains	9.7	23.6	SF_6
			silage-based diet	23.8	17.4	GF

Table 1 (*continued*)

Reference	Animal breed	BW, kg/animal	Ration type	DMI[2], kg/d per animal	CH_4[2], g/kg DMI	Technique used
Bharanidharan et al. (2018)	Holstein	540.3	TMR	12.3	11.3	IRC
			roughage, concentrate	10.2	10.3	
Dini et al. (2012)	Holstein	536.2	legume-dominated	17.3	29.4	SF_6
			grass-dominated	16.8	31.0	
Hammond et al. (2014)	Holstein/Friesian	339.8	rye grass	8.03	28.4	SF_6
			RC	7.06	28.0	
			BT	7.61	28.9	
Hristov et al. (2015)	dairy cow	653	control ($n = 7$)	26.7	20.4	GF
			TCNSL[4] ($n = 7$)	26.6	18.9	GF
Grainger et al. (2007)	Holstein-Friesian	496.6	ryegrass	19.9	21.8	SF_6
Lee et al. (2004a)	Holstein/Friesian		ryegrass with no WC	15.6	21.7	SF_6
			ryegrass + 15% WC	17.6	20.9	
			ryegrass + 30% WC	18.6	18.6	
			ryegrass + 60% WC	20.5	18.1	
Odongo et al. (2006)	Holstein cow	620.6	dairy TMR	19.7	23.3	IRC
			dairy TMR + 24 mg Rumensin	19.1	22.4	
Olijhoek et al. (2017)	Holstein	647.6	high-RFI/low-concentrate	20.9	30.7	IRC
			high-RFI/high-concentrate	23.7	21.4	
			low-RFI/low-concentrate	18.6	32.4	
			low-RFI/high-concentrate	21.6	24.5	
	Jersey	469.2	high-RFI/low-concentrate	15.0	32.6	
			high-RFI/high-concentrate	17.8	28.2	
			low-RFI/low-concentrate	14.9	32.5	
			low-RFI/high-concentrate	17.0	27.9	
Rischewski et al. (2017)	Holstein	655	TMR + silages			
			period I	16.9	20.0	GF
			period II	20.6	18.4	
			period III	20.1	20.7	
Wims et al. (2010)	Holstein/Friesian	493.8	mixed forage			SF_6
			low-forage mass[5]	16.9	17.0	
			high-forage mass[5]	15.4	18.7	
Woodward et al. (2002)	Friesian/Jersey		ryegrass	13.1	19.3	SF_6
			sulla	10.7	24.3	
Woodward et al. (2004)	Friesian	538	ryegrass	14.9	24.2	SF_6
			ryegrass + PEG	14.9	24.7	
			BT	17.4	19.7	
			BT + PEG	17.1	22.9	
Waghorn et al. (2016)	Holstein/Friesian	520	LSR[6] ($n = 4$ periods)	15.4	21.8	GF
			HSR[6] ($n = 4$ periods)	13.7	22.7	

DMI = dry matter intake; RFI = residual feed intake; GF = GreenFeed system (C-Lock Inc., Rapid City, SD, USA); IRC = indirect respiratory chamber; SF_6 = sulfur hexafluoride tracer technique; TMR = total mixed ration; WDGS = wet distiller's grains with solubles; DDGS = dry distillers' grains with solubles; SS = sorghum silage; RC = red clover (*Trifolium pratense*); BT = birdsfoot trefoil (*Lotus corniculatus*); WC = white clover (*Trifolium repens*); PEG = polyethylene glycol.

[1] All data are presented in their original units of the literature. A graphical comparison of calculated CH_4 missions per DMI is presented in Fig. 2.

[2] Dry matter intake and CH_4 yield were used to calculate daily CH_4 emissions. Animals of different ages and BW were used in the dairy and beef data sets, with correspondingly different DMI and CH_4 production values.

[3] Wild flowers are mixtures of a ryegrass (*Lolium perenne*) and flowers (Hammond et al., 2014).

[4] TCNSL is the basal diet with 30 g/cow per day of technical grade cash-nut-shell liquid (data collected from 7 cows).

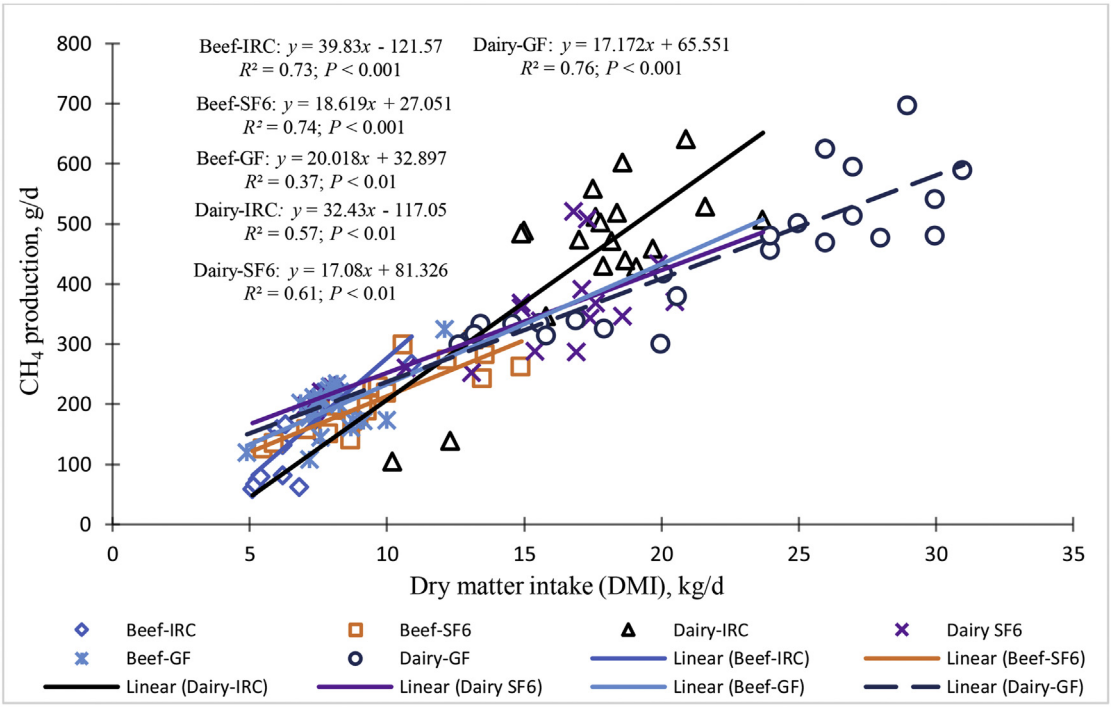
[5] Low-forage mass, 100 kg DM/ha; High-forage mass, 2,200 kg DM/ha.

[6] LSR and HSR means low- and high-stocking rates.

(19.1 g/kg DMI; Hristov et al., 2013a, b; Clark et al., 2005) for CH_4 estimation from beef and dairy cattle. Animals of different ages and body weights were used in the dairy and beef data sets, with correspondingly different DMI and CH_4 production values. Measurements in the dairy dataset were from lactating Holstein-Friesian dairy cows with a high DMI and high CH_4 production, whereas measurements in the beef dataset were from growing/finishing steers or non-lactating heifers with lower DMI and low CH_4 production. Therefore, it makes direct comparisons more difficult because the DMI ranges are varied between dairy and beef cattle. It is also difficult to measure the DMI on animals grazing in natural environment. However, Eq. (1), based on the data from Table 1 and presented in Fig. 2B, provides a rather simple means to estimate daily CH_4 production by cattle based solely on their DMI when no other information is available. An R^2 of 82% implied that DMI strongly influenced CH_4 production. Since most dairies and feedlots know their cattle's DMI, an inventory of CH_4 emission is possible.

Most national inventories assume CH_4 production is linear with DMI (Hristov et al., 2013b; Miller et al., 2013; Niu et al., 2018). This assumes that CH_4 production is constant for all DMI values and there is a 0-intercept in the prediction equation (Charmley et al., 2016). However, Cottle and Eckard (2018) reported that the differences in CH_4 production values from beef cattle studies using different CH_4-measurement methods, cattle breeds, diets, and geographic location are so diverse that a universal CH_4 production value may not be recommended at this stage. This agrees with our current study which indicated that the 3 different CH_4-measurement methods (IRC, SF_6, and GF) may misrepresent the relationship between daily CH_4 production and DMI (g/kg DMI; Fig. 2A). Based on the present study, average estimate of CH_4 production (g/d) varied among the 3 measurement techniques, mean (±SE) values were 39.8 ± 5.48 (beef-IRC), 18.6 ± 2.36 (beef-SF_6), 20.0 ± 6.86 (beef-GF) for beef cattle, and 32.4 ± 3.33 (dairy-IRC), 17.1 ± 6.40 (dairy-SF_6), and 17.2 ± 2.22 (dairy-GF) for dairy cattle. Overall CH_4 emissions determined using GF and SF_6 were significantly lower ($P < 0.05$) than those measured using IRC technique. Differences in daily CH_4 production between GF and other techniques are likely due to the short duration of the CH_4 measurements obtained for

A



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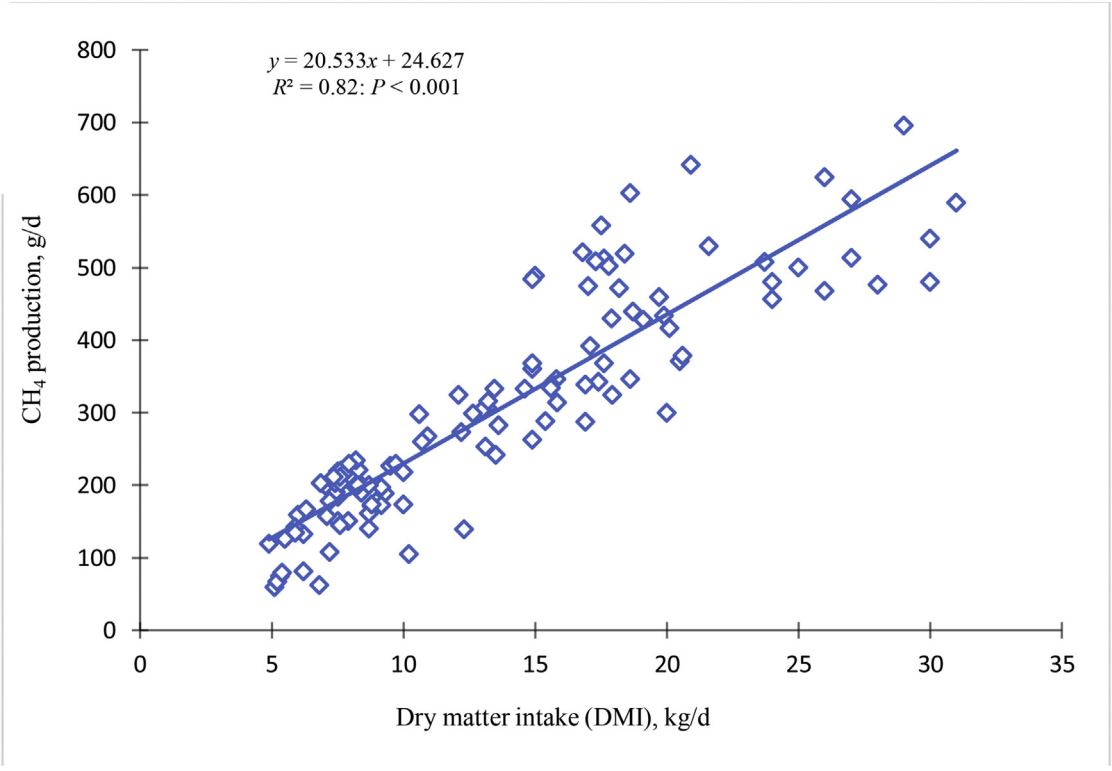

Fig. 2. Selected studies of methane emissions from widely used techniques. (A) Effects of dry matter intake (DMI) on daily CH_4 emissions in dairy and beef cattle associated with detection methods, and (B) effects of DMI on average daily CH_4 emissions in dairy and beef cattle. SF_6 = sulfur hexafluoride tracer technique; IRC = indirect respiration chamber; GF = GreenFeed system (C-Lock Inc., Rapid City, SD, USA). Source: adapted from Table 1.

each animal (Hammond et al., 2015). The variation in DMI for beef cattle with the GF was much smaller than the variation in measured CH_4 production with that system, which likely was a large contributor to the low R^2 value. An argument in support of the GF measurement systems is that data are collected several times over the course of a day to arrive at an estimated daily emission rate. The

GF measurements can be made over days and weeks, whereas other techniques are difficult to implement for more than a few days due to high labor costs. A limitation of GF and SF_6 breath measurement systems is how could CH_4 production from the hind gut be measured with GF and SF_6 (Murray et al., 1976, 1978). Using an isolated tracer method and cannulated sheep, Murray et al. (1976, 1978) estimated that the hindgut of ruminants produces approximately 11% to 13% of total enteric CH_4 emissions. Two explanations for lower values of GF and SF_6 are possible: 1) CH_4 production by the hindgut is much greater impact; 2) CH_4 losses from hindgut are being measured (Murray et al., 1978) despite the precautions that are taken to prevent such occurrence. As with all short-term CH_4-measurement techniques, cumulative daily CH_4 production may be under- or over-estimated because of diurnal patterns in CH_4 emission rate over a 24-h period — emissions will differ based on animal activity, time since feeding, and other factors (Hammond et al., 2016b). Strong diurnal patterns of ruminal concentrations of VFA, pH, and bacterial community changes have been reported in sheep (Kristensen et al., 1996) and dairy cows (Palmonari et al., 2010). However, all 3 methods support that: 1) DMI is a strong determinant of CH_4 production, and 2) the average rate of CH_4 production is between 15 and 25 g per kg of DMI.

5.2. Feed conversion efficiency and CH_4 emissions

In one investigation, Fox et al. (2001) confirmed that a 10% improvement in FCE had a much greater impact on feedlot profitability than a similar improvement in average daily gain (ADG; Table 2). Results from Table 2 indicated that a 10% increase in ADG improved estimated profits by 18% compared to a control. In contrast, when DMI remained the same and there was a 10% improvement in FCE, ADG increased by 11%, and resulted in a 43% increase in estimated profits. Therefore, genetic selection for animals that have a superior FCE (e.g., efficient cattle) could potentially increase profits more than selection for a higher ADG.

It has been shown that both FCE (heritability [h^2] = 0.29) and net feed efficiency (NFE; $h^2 = 0.39$) are moderately heritable in growing Angus cattle (Table 3). Therefore, it may be possible to selectively breed cattle that ingest less feed without reduced performance because of improvements in feed efficiency (Carstens, 2019), which would lead to increased cost-effectiveness. However, selecting dairy cows for feed efficiency and lower emissions may be more difficult than it is for beef cattle because of a host of factors need to be considered, such as stage of lactation, milk components, somatic cell counts, body condition score, feed efficiency and feed intake. Therefore, one alternative strategy of mitigating CH_4 emission might involve selective breeding for animals that are lower CH_4 emitters because of higher FCE, resulting in lower energy losses as CH_4. However, such a strategy has yet to be evaluated.

Table 2
Effect of improvement in average daily gain (ADG) and feed conversion efficiency (FCE) on steer profitability[1].

Item	Average	10% higher ADG	10% higher FCE[2]
DMI, kg/d	8.5	9.1	8.5
ADG, kg/d	1.45	1.60	1.63
Feed to gain	5.86	5.68	5.21
Feed cost, $	176	172	157
Non-feed cost, $	98	91	89
Total cost of gain[3], $	274	263	246
Profit, $	65	77	93

DMI = dry matter intake.
[1] Computed with Cornell Value Discovery System (Tedeschi et al., 2001; Fox et al., 2001).
[2] FCE is the ratio of feed to gain.
[3] Total cost of gain = Feed cost + Non-feed cost.

Table 3
Heritability (h^2) estimates (±SE) and genetic correlations among growth and efficiency traits in Angus cattle[1].

Trait	ADG	BW	DMI	FCE	NFE or RFI
ADG	0.28 ± 0.04	0.53 ± 0.07	0.54 ± 0.06	−0.63 ± 0.06	−0.04 ± 0.08
BW	–	0.04 ± 0.01	0.65 ± 0.03	−0.01 ± 0.07	−0.06 ± 0.06
DMI	–	–	0.39 ± 0.03	0.31 ± 0.07	0.69 ± 0.08
FCE	–	–	–	0.29 ± 0.04	0.66 ± 0.05
NFE	–	–	–	–	0.39 ± 0.03

ADG = average daily gain; BW = body weight; DMI = dry matter intake; FCE = feed conversion efficiency (feed DMI per unit weight gain); NFE = net feed efficiency; RFI = residual feed intake.
[1] Adapted from Arthur et al. (2001). n = 1,180 young Angus bulls and heifers.

5.3. Residual feed intake (RFI) and methane emissions

Traditionally, beef cattle efficiency measures were dependent on FCE, the ratio of feed intake to ADG. Animals with a low FCR consume less feed per kilogram of ADG, whereas animals with higher FCR consume more feed per unit of ADG. However, the primary limitation of FCR is that it represents a gross measure of feed intake; it does not evaluate yet between maintenance and growth requirements (Carstens and Tedeschi, 2006). In contrast, RFI is a measure of feed efficiency that is calculated as the difference between actual and expected feed requirements, which is obtained from feeding beef total mixed ration diet, or regression for BW maintenance against some measure of production for meat and milk (Koch et al., 1963; Arthur et al., 2001; Basarab et al., 2003; Nkrumah et al., 2006). The RFI is identified as the measure of method when determining efficiency in beef cattle (Table 3; Nkrumah et al., 2006; Hegarty et al., 2007; Herd and Arthur, 2009). However, the relationship between RFI and CH_4 emissions in beef and dairy cattle is weak (Waghorn and Hegarty, 2011). Hegarty et al. (2007) reported a significant relationship between CH_4 emission and RFI for Angus steers. However, RFI accounted for only a small proportion of the variations in CH_4 production. The data suggest that animal selection could only reduce CH_4 loss per kilogram of DMI by 10% to 20% (Waghorn et al., 2006). Myer et al. (2017) also reported that genetic markers associated with RFI and feed efficiency have been difficult to identify, and differing genetics, feed supplementation, and environments among studies contribute to great variation and elucidation of results.

The relationships between DMI and CH_4 emissions (g/d) in low-RFI ($y = 24.5x + 0.34$; $R^2 = 0.64$; $P = 0.01$) and high-RFI ($y = 24.17x - 1.59$; $R^2 = 0.64$; $P = 0.01$) beef cattle are presented in Fig. 3. The results indicate that there was no significant reduction in CH_4 as a function low-RFI (<0; more efficient) and high-RFI (>0; less efficient) beef cattle. These findings demonstrate that differences in CH_4 production may not be directly associated with RFI, but rather they are due to RFI-induced differences in DMI (Freetly et al., 2015). However, several studies have shown a positive relationship between RFI and CH_4 production but the effect of RFI on CH_4 is not consistent across all studies (Freetly and Brown-Brandi, 2013; Carberry et al., 2014; McDonnell et al., 2016; Flay et al., 2019). If animals are selected for reduced methane production, feed efficiency will be increased by the amount of energy conserved from CH_4 production, which is small. However, there are several physiological mechanisms, which have no effect on CH_4 production, that can result in increased feed efficiency as discussed by Herd and Arthur (2009). Selection for efficiency is probably mostly by these mechanisms and in some cases by reduction in CH_4 production. Waghorn and Hegarty (2011) reported no differences in CH_4

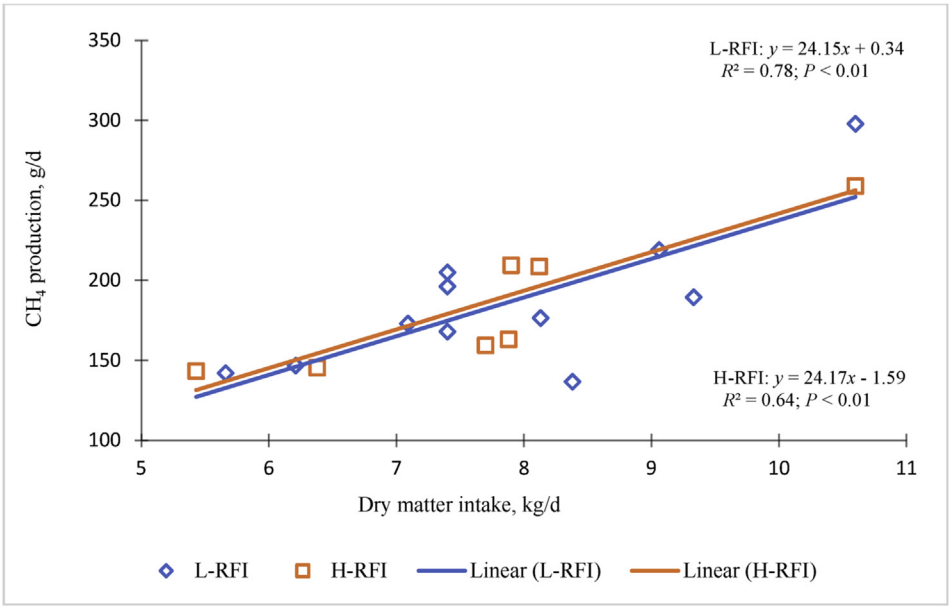

Fig. 3. Feed dry matter intake and methane production from beef cattle selected for variance in residual feed intake (RFI). Low (L)-RFI are efficient, high (H)-RFI are inefficient. RFI is expected feed requirements for maintenance and growth, with the expected feed requirements obtained by regression of feeding standards formula. IRC = indirect respiratory chamber; GF = GreenFeed system (C-Lock Inc., Rapid City, SD, USA). Sources: Dini et al. (2019; beef, BW = 357 kg BW; SF_6); Hegarty et al. (2007; beef, BW = 590 kg; SF_6); Alemu et al. (2017; beef heifers, BW = 380 kg; IRC and GF); Mercadante et al. (2015; cattle, BW = 238 to 326 kg BW; SF_6); Flay et al. (2019; dairy cattle, BW = 448 kg; GF); Lansink, (2018; beef, BW = 269 kg; GF).

production among dairy cows with differing RFI, which is similar to the findings in Fig. 3. Comparable results were reported by McDonnell et al. (2016), in which CH_4 production did not differ between heifers with high- and low-RFI. When adjusted for DMI, CH_4 yields (g/kg DMI) were similar for high- and low-RFI heifers, using GF method (27.7 and 28.5 g/kg DMI, respectively) and respiration chambers (26.5 and 26.5 g/kg DMI, respectively; Alemu et al., 2017). Recently, Flay et al. (2019) reported that RFI did not affect either CH_4 emission per day or CH_4 emission per kilogram BW in dairy heifers; however CH_4 emission per kilogram of DMI was higher in low-RFI heifers than high-RFI heifers because of their lower DMI. No differences in abundances of methanogen species were observed between animals ranked as both substrates have a higher or lower RFI across 2 dietary energy concentrations (a low energy + high forage vs. a high energy + low forage) (Carberry et al., 2014). However, Zhou et al. (2009) reported a greater proportion of *Methanosphaera stadtmanae* and *Methanobrevibacter* sp. AbM 4 in high-RFI cattle compared to low-RFI cattle. Miller et al. (1986) explained that *M. stadtmanae* utilizes methanol, whereas *Methanobrevibacter* sp. AbM4 utilizes acetate as its main substrate for CH_4 production (Zhou et al., 2009, 2010). These results suggest beef cattle with microbiomes prefer organic methanogenesis substrates with a higher RFI (Basarab et al., 2013). It is also important to note that differences in dietary energy concentration can affect associations between RFI and overall methanogen profiles in Hereford × Aberdeen Angus steers (Zhou et al., 2010).

5.4. Interaction of rumen microbiota with other parameters

Animals that consumed a concentrate-based diet had lower CH_4 emissions than those fed a forage-based diet (Wallace et al., 2014; Roehe et al., 2016). This variation was due to higher propionic acid production [decrease A:P ratio] from digestible carbohydrates in the rumen, which leads to reduction of H_2 available for typical CH_4 producing pathway (Beauchemin and McGinn, 2005; Cottle and Eckard, 2018). Thus, CH_4 reduction strategies that reduce available H_2 may be antagonistic to cellulose digestion (Wolin et al., 1997). In addition, lower A:P ratios and higher phylum Firmicutes populations related to higher ADG (Waghorn and Barry, 1987; Myer et al., 2015). Recently, Kim et al. (2018) reported that supplementation of acetogenic bacteria isolated from Korean native goats decreased methanogenic archaea. Acetogens undertake reductive acetogenesis, which is a substitute for the typical H_2-using pathway; therefore, acetogens may function as a net H_2 sink that reduces CH_4 emissions (van Nevel and Demeyer, 1996). However, the primary cellulolytic bacterial species and protozoa in the rumen are H_2 producing microbes; thus, counteracting CH_4 reduction strategies that reduce available H_2 may slow cellulose digestion (Latham and Wolin, 1977; Ungerfeld, 2015).

The number of methanogenic archaea may not be a strong determinant of CH_4 production, but rather the metabolic activity of individual methanogenic species (Shi et al., 2014). However, Wallace et al. (2014, 2015) reported that the ratio of archaea to bacteria in the rumen could be used to estimate CH_4 emissions ($R^2 = 0.49$) in beef cattle fed high- and medium-levels of concentrate in their diets. These authors argue that methanogenesis is the only mechanism of ATP synthesis for methanogens and therefore, there should be a relationship between CH_4 production and the concentration of methanogens in the rumen. A positive correlation between CH_4 production and abundance of *Methanobrevibacter* species has been reported in dairy cows (Danielsson et al., 2012, 2017). This agrees with data from present study which indicated that a positive correlation exists between populations of total protozoa ($R^2 = 0.55$; $P < 0.04$; Fig. 4A) and total bacterial population ($R^2 = 0.46$; $P < 0.05$; Fig. 4B) per unit of forage-based DMI and CH_4 emissions (g/d) in sheep and goats. In addition, CH_4 production was strongly correlated with Firmicutes-to-Bacteroidetes ratio (F:B) (Fig. 4C) and total methanogens (Fig. 4D). A similar relationship between the relative abundance of *M. gottschalkii* and high CH_4 production, and the relative abundance of *M. ruminantium* and low CH_4 production, have been reported (Shi et al., 2014; Danielsson et al., 2017) in sheep and dairy cattle.

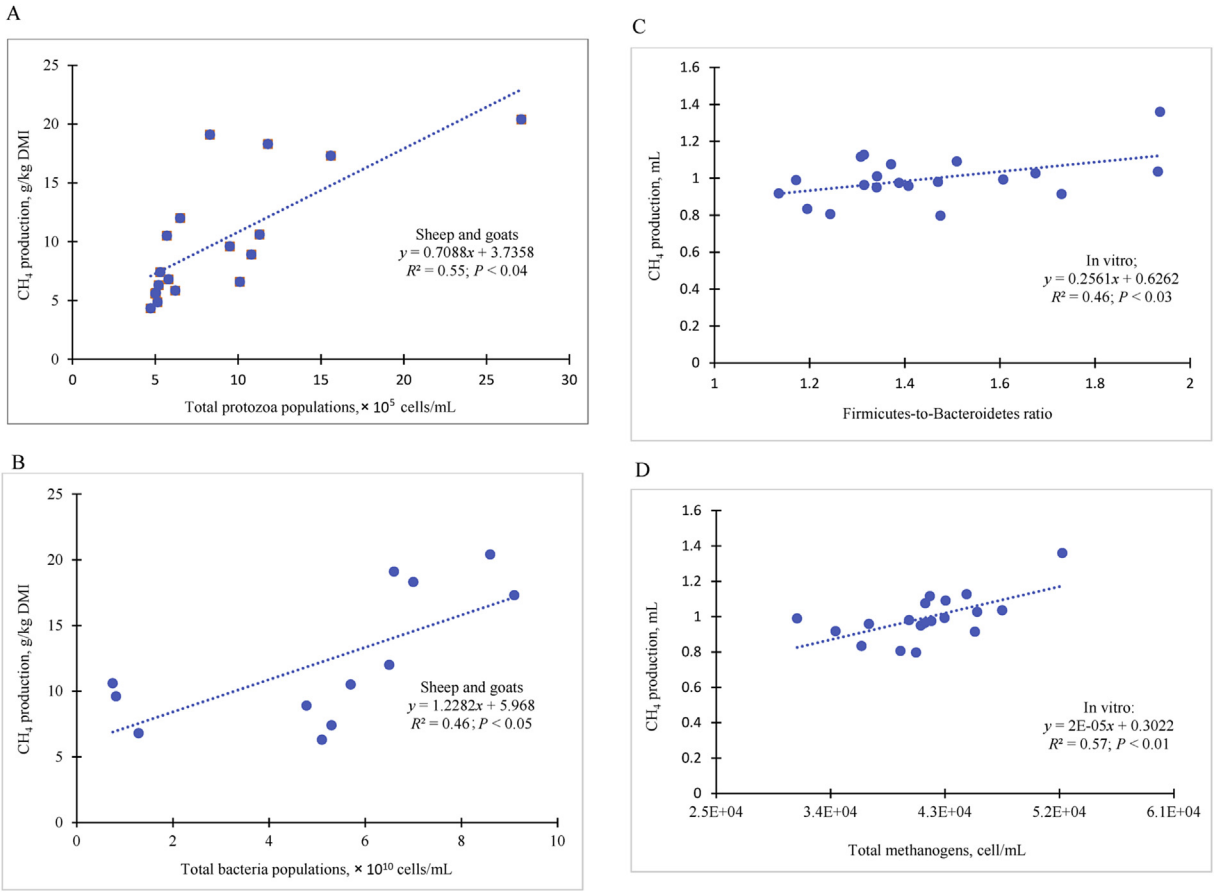

Fig. 4. Effects of predominant bacterial phylum, total protozoa, and methanogen on methane emissions (A) Relationships between CH_4 productions and populations of total protozoa, (B) total bacteria, (C) Firmicutes-to-Bacteroidetes ratio, and (D) total methanogens in the rumen and in vitro rumen incubations. Source: Animut et al. (2008a, b; respiratory chamber), Liu et al. (2011; respiratory chamber), Puchala et al. (2005, 2012a, b; respiratory chamber), Min et al. (2019a; in vitro).

A possible explanation for this could be competition for the same substrate, as *Methanobrevibacter* species are hydrogenotrophs (Leahy et al., 2013) and use H_2 and/or formates as substrates for CH_4 production. Therefore, different methanogenic species could have an advantage at different H_2 concentrations and/or respond differently (because of different methanogenic enzymes; Reeve et al., 1997) to produce CH_4 (Kittelman et al., 2014). These results implied that the dominant types in the rumen microbial community (F:B ratio), total protozoa, and total methanogen populations might have a role in adapting host biological parameters to reduce CH_4 production and can potentially be utilized to estimate CH_4 emissions (Chen et al., 2017). Chen et al. (2017) reported that the abundances of Firmicutes and the F:B ratio were strongly correlated with reduced CH_4 production. These same authors stated that Firmicutes populations were linked to lower VFA levels when CH_4 production was high, indicating that the F:B ratio could be used as an indicator to study gut microbiome and GHG emissions. Addition of tannins in the diets increased Firmicutes and F:B ratio in the rumen (Min et al., 2014a; Carrasco et al., 2017), which improved ADG due to lower A:P ratio and CH_4 production (Min et al., 2019a, b). However, Wright et al. (2009) attributed modifications in methanogenic diversity to dietary alteration, whereas other studies reported that variations in methanogenic diversity were due to DMI (Ungerfeld, 2018), diet composition (Wright et al., 2009), host traits (Zhou et al., 2010; Roehe et al., 2016), and geographical range (Henderson et al., 2015). Recently, Roehe et al. (2016) reported that methanogenesis genes (e.g., methyl coenzyme M reductase [*mcrA*] and molybdenum formylmethanofuran dehydrogenase B [*fmdB*]) were coupled with CH_4 emissions, but host microbiome cross talk genes (e.g., GDP-L-fucose synthetase [*TSTA*3] and L-fucose isomerase [*Fucl*]) were related to FCE. Published data also showed that higher rumen particulate passage was linked with lower rumen H_2 concentrations, reduced CH_4 generation, and increased propionate production (Janssen, 2010). Dairy cows which consumed a white clover legume silage had a higher level of milk production, higher rates of rumen passage and fermentation and higher levels of voluntary feed intake than cows consuming grass silage (Thomson et al., 1985; Auldist et al., 1999; Dewhurst et al., 2003). Different feeds produce different ruminal passage rate (Owens and Hanson, 1992). To understand digestion of different feeds, it is important to know rates of passage. However, little work has been done on differences in passage rates among types of forage diets and CH_4 production per unit of DMI per day.

5.5. Other strategies for methane emissions

Several potential enteric CH_4 mitigation strategies (Fig. 5) have been proposed, including use of CH_4 inhibitors (e.g., halogenated compounds, nitrate), probiotics (e.g., yeast, acetogen probiotics), oilseeds, essential oils, dietary fat, micro-algae, plant constituents (e.g., tannins, saponins), propionate enhancers, immunization against CH_4 oxidation, improvements in forage quality, and genetic selection of low CH_4 producing ruminants (Beauchemin et al., 2008; Hristov et al., 2013a, b). Ionophores have not been

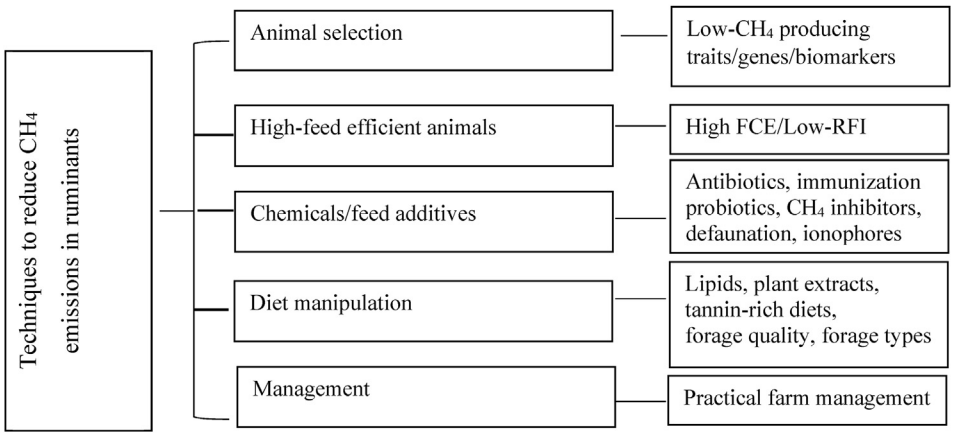

Fig. 5. Methane emission abatement strategies for ruminants. FCE = feed conversion efficiency, RFI = residual feed intake. Low (L)-RFI are efficient, high (H)-RFI are inefficient. RFI is expected feed requirements for maintenance and growth, with the expected feed requirements obtained by regression of feeding standards formula. Sources: Arthur et al. (2001), Beauchemin et al. (2007, 2008), Broucek (2018), Charmley et al. (2016), Carstens, (2019), Hegarty et al. (2007), Hristov et al. (2013a, b), Min and Solaiman (2018), Nkrumah et al. (2006), Patra et al. (2017), Roeche et al. (2016), Ross et al. (2013), Tavendale et al. (2005), and Woodward et al. (2001).

proposed but have been used for more than 40 years commercially. The most effective strategy for reducing CH_4 emissions will likely incorporate several of these mitigation strategies (Beauchemin et al., 2008). These approaches have emerged as means to decrease CH_4 production; however, additional studies are needed before these practices can be recommended to livestock producers.

6. Plant tannins and methanogenesis

6.1. Tannins

Plant tannins occur primarily as condensed (CT) and hydrolysable tannins (HT) (Hagerman et al., 1992). Condensed tannins (or proanthocyanidins) are polyphenolic compounds of flavan-3-ol units (e.g., catechin subunits). The numerous phenolic groups in tannins can bind to various substrates (e.g., proteins, metal ions and polysaccharides) to form indigestible complexes (Haslam, 1989; Hagerman et al., 1992). Both CT and HT are varied among forages. Tannins are thought to have both beneficial and detrimental effects on feed nutritive value and animal performance. The influence of CT in the diet on the ruminal microbiota, CH_4 emissions, and ruminal fermentation have been reported (Min et al., 2003b; Carulla et al., 2005; Grainger et al., 2009). Plant tannins, as feed supplements or as tanniferous forage diets, have shown a potential for reducing enteric CH_4 emissions by up to 20% (Woodward et al., 2001; Waghorn et al., 2002). However, tannin-rich diets (>5% DM) can negatively affect animal production when dietary crude protein (CP) is a limiting factor, because tannins reduce absorption of amino acids in the small intestine (Waghorn, 2008).

Unlike CT, HT (e.g., gallic acid or ellagic acid) are hydrolyzed after ingestion, gallic acid and its degradation products are absorbed from the small intestine of animals and are possibly poisonous to ruminants (Hagerman et al., 1992). Strategies for formulating optimal tannin-rich diets for mitigation of enteric CH_4 emissions from ruminants, without biological impacts on ruminant animal productivity, have not been established. Therefore, attention must be given so that the advantages of decreased CH_4 emissions are not offset by negative properties of tannins on feed intake, digestion, metabolism, and animal productivity.

6.2. Tannin-rich diets as a potential methane mitigation strategy

Research on CH_4 inhibition strategies associated with tannin-rich diets or CT extracts in vivo have been conducted with sheep (Waghorn et al., 2002; Woodward et al., 2001, 2002; Sliwinski et al., 2004; Tiemann et al., 2008), dairy cows (Woodward et al., 2001, 2002; Beauchemin et al., 2007), goats (Puchala et al., 2005; Animut et al., 2008a, b), and beef cattle (Krueger et al., 2010). Despite this research, mechanisms of associative effects of CT and methanogenesis are not well understood. A reference scaling factor per unit of DMI is needed to compare CH_4 emissions of varying tannin-rich diets (e.g., Sericea lespedeza) in both in vitro and in vivo settings. The relationship between CT (% DM) and reduces CH_4 production per unit of DMI (Fig. 6) indicated that increasing CT in the diets linearly reduced CH_4 emissions in meat goats ($y = -0.769x + 21.91$: $R^2 = 0.79$; $P < 0.01$). This has been confirmed by the findings that predominant species of *Methanobrevibacter* spp (75%) were linearly decreased with increasing CT-containing pine bark (1.6% to 3.2% CT DM) concentration (Fig. 7), similar to that reported by Liu et al. (2011) and Min et al. (2015a) in sheep, goats, and beef cattle.

Dairy cows fed diets composed of CT-rich birdsfoot trefoil (*Lotus corniculatus*; 2.62% CT DM) had reduced CH_4 production (g/kg DMI) by 13% to 16% (Woodward et al., 2004). When wattle tannins (*Acacia mearnsii*; 2.5% CT DMI) were offered to sheep fed a ryegrass-based diet (Carulla et al., 2005), CH_4 emissions were decreased by 13%. Grainger et al. (2009) reported that CH_4 production (g/d) dropped by 14% at a low level of CT supplementation (163 g/d) and by 29% when fed at a higher level (CT at 244 g/d) in grazing dairy cows. Types of CT may not only affect CH_4 production, but also have effect on the microbial community and ruminal fermentation. In addition, diets composed of CT-rich birdsfoot trefoil (Turner et al., 2005) and other CT-rich pasture species (Strom, 2012) can increase the concentration of omega-3 fatty acids (e.g., linoleic and linolenic acids) in beef adipose tissue via changing ruminal biohydrogenation of fatty acids, suggesting that CT in diets may produce potentially value-added milk in the future (Khiaosa-Ard et al., 2015).

Dairy cows fed diets composed of CT-rich birdsfoot trefoil silage or perennial ryegrass (*Lolium perenne*) silage had similar total CH_4 emissions, but total CH_4 emissions were 13% lower (g DM) from cows and 15% lower per unit of milk solids (378 vs. 434 g/kg milk solids; Woodward et al., 2001). Woodward et al. (2002) reported CH_4 production of 24.6 g/kg DMI when dairy cows were grazing perennial ryegrass pasture, compared to CH_4 (19.5 g/kg DMI) with CT-rich sulla (*Sulla coronaria*; 3.5% to 6.7% CT DM). In addition to the impact on methanogenesis, CT-rich diets fed to ruminants can have other beneficial effects on animal production (Min et al., 2003b, 2005a, b; Hoskin et al., 2003), smaller populations of

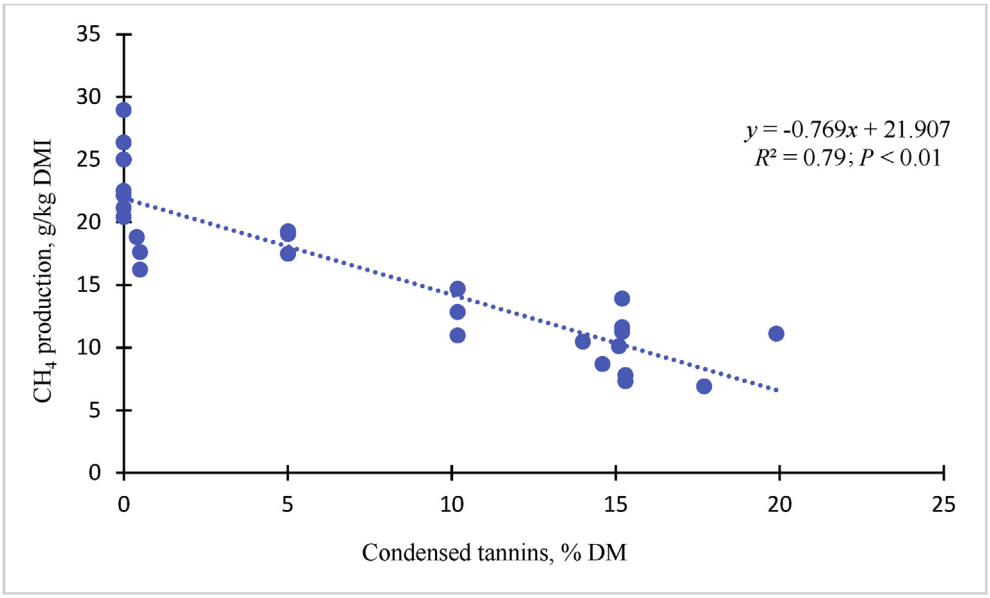

Fig. 6. Effect of condensed tannin-rich diets on rumen methane production per kilogram of dry matter intake for meat goats. Sources: Animut et al. (2008a, b); Puchala et al. (2005, 2012a, b).

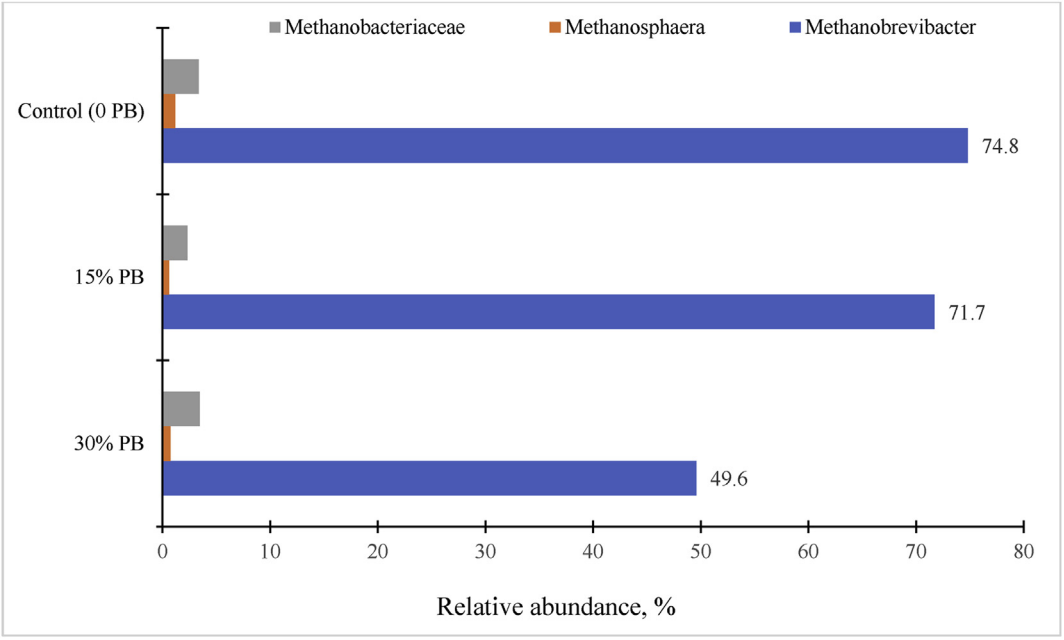

Fig. 7. Relative abundance (%) of major gastrointestinal methanogenic archaea diversity (>0.9%) present in meat goats ($n = 6$) fed condensed tannins (CT)-containing ground pine bark (PB) supplementation with grain mixed diets as analyzed using pyrosequencing. Control, 0 PB, 19% CT DM; 15% PB, 1.63% CT DM; and 30% PB, 3.20% CT DM, as-fed basis (Min et al., 2014b).

gastrointestinal nematodes (Min and Hart, 2003) and improved milk quality through increased concentrations of unsaturated fatty acids (Turner et al., 2005).

Generally, the most successful enteric CH_4 mitigation strategies utilizing tannins, without any detrimental effects on animal productivity, have been documented with diets that contained high levels of CP in the forages, this was 15% to 25% CP from birdsfoot trefoil, big trefoil (*Lotus pedunculatus*), sulla, sericea lespedeza (*Lespedeza cuneate*), and high-quality perennial ryegrass (*L. perenne*). Min et al. (2005a) studied steers grazing winter wheat forage (15% to 18% CP) with quebracho CT extract at 10 to 20 g/kg DMI. In vitro CH_4 production was reduced by 25% to 51% (Min et al., 2005a, 2006b). It appears that a CT-rich diet can effectively decrease CH_4 emissions per unit of DMI over a range of CP from 15% to 25%. Previous in vitro research showed that addition of plant secondary metabolites, such as CT extract (quebracho) and saponin, reduced CH_4 production by 6% to 40% per unit of DM (Min et al., 2015a; Goel and Makkar, 2012). Min et al. (2015a) reported linear reduction of CH_4 in the presence of quebracho (*Schinopsis lorentzii*), mimosa (*Albizia julibrissin*), chestnut (*Castanea dentata*) and saponin (*Yucca schidigera*) extracts, with increasing concentrations of plant-derived secondary metabolites. Similarly, Becker et al.

(2014) reported an inhibition of CH_4 production in an in vitro experiment that was linearly related with the concentration of extracted CT (e.g., catechin). They also reported that 6 hydrogen atoms per catechin molecule were retained by purified CT, and CH_4 production was decreased at a rate of 1.2 mol of CH_4 per mole of catechin (Becker et al., 2014).

Dominant ruminal cellulolytic bacterial species, including *Fibrobacter succinogens*, *Ruminococcus albus*, and *Ruminococcus flavefaciens* (Koike and Kobayashi, 2009), may influence CH_4 production (Chaucheyras-Durand et al., 2010). Min et al. (2006a) reported that cultures from *R. albus* and *R. flavefaciens* produced the most H_2 among dominant ruminal cellulolytic bacterial strains. In addition, these cellulolytic bacteria resulted in greater CH_4 production when cultured with *M. smithii* compared with other co-cultured combinations. More recent research indicated that tannin-rich diets resulted in ruminal CH_4 suppression through reduced methanogen population size (Min et al., 2014a, b; Christensen et al., 2017) and decreased H_2 production in the rumen (Tavendale et al., 2005). Tavendale et al. (2005) reported that CT extracted from big trefoil inhibited methanogen growth rates in broth cultures, especially *M. ruminantium* strains.

6.3. Effects of tannin-rich diets on rumen fermentation and microbiota

The CT bind with plant proteins in the rumen because of its neutral pH, but CT-protein complexes dissociate in the acidic pH of the abomasum (Hagerman et al., 1992; Min et al., 2003). The extent to which CT interferes with protein digestion is a function of astringency, concentration, and potential sites for binding (Haslam, 1989; Hagerman et al., 1992; Waghorn, 2008). In vitro and in vivo studies have consistently shown a reduction in the growth rate of select strains, as well as increased proteolysis, as a consequence of dietary CT (McNabb et al., 1996; Molan et al., 2001; Min et al., 2005a, b). However, some strains (*Clostridium proteoclasticum* $B316^T$ and *R. albus* 8) showed transient increases in their growth rate at low concentrations (50 to 100 μg/mL) but not at high (>200 μg/mL) concentrations of CT (Min et al., 2005b).

In general, concentrations of VFA are known to affect CH_4 production; higher concentrations of propionate and lower concentrations of acetate have been found to reduce CH_4 emissions (Monteny et al., 2006). Rumen A:P ratio may also be associated with a lower CH_4 production per unit of DMI in ruminants. As ruminal VFA production changed towards less production of acetate relative to propionate (i.e., lower A:P ratio), the net concentrations of H_2 in the rumen decreased via physical intracellular hydrogenosomes, resulting in less CH_4 being formed (van Nevel and Demeyer, 1996).

Tannin-rich diets can modify the rumen fermentation profiles and ruminal bacterial community diversity. Complexes of CT-protein are most commonly based on hydrophobic and hydrogen bonding in a pH dependent manner (Haslam, 1989). When CT-containing forage is consumed, CT-substrate complexes form during the processes of chewing and ruminating (Jones and Mangan, 1977). Once it across the rumen, CT can also bind to substrates (e.g., protein) and bacterial cell surfaces (Jones et al., 1994). Dietary CT (e.g., sainfoin) has been shown to induce changes in the activity of endoglucanase, the enzyme responsible for breaking internal glycoside bonds in a glucose polymer, and morphology (physical) of several species of rumen bacteria (Chiquette et al., 1988; Bae et al., 1993). Inhibition of rumen bacteria by CT is probably due to interactions between CT present in the tannin structure and the specific substrate to which it binds (e.g., protein, bacterial cell walls, etc.) (Bae et al., 1993). The addition of CT extracts to the diet reduced populations of CH_4-producing archaea and some cellulolytic bacteria (*R. flavefaciens*) (Bhatta et al., 2009). Ruminal fungi and protozoa have been linked to CH_4 formation (Khiaosa-Ard et al., 2015). The process of protozoal CH_4 formation is via hydrogenosomes. This protozoa-derived H_2 was associated with methanogens in the rumen (Mosoni et al., 2011). To enhance access to H_2, these methanogens may be involved in a mutually beneficial relationship with rumen protozoa (Finlay and Fenchel, 1989). It has been shown that nearly 37% of CH_4 from ruminants is produced by protozoa-associated methanogens (Finlay et al., 1994). Tymensen et al. (2012) confirmed that numbers of *Methanobrevibactor* spp. were high among the community of protozoa-associated methanogens. Furthermore, the population of methanogens was reduced when ruminants were fed diets containing CT-enriched from birdsfoot trefoil (2.7% to 4.9% CT DM; Christensen et al., 2017) and pine (*Pinus*) bark CT (1.6% to 3.3% CT DM) (Min et al., 2014a, b). However, a reduction in CH_4 production is not always concomitant with decreased protozoa (Bhatta et al., 2009), as some tannins, e.g. peanut (*Arachis hypogaea*) skin CT, may decrease methanogens that are not associated with protozoa (Min et al., 2019a). Inclusion of wattle tannin extracts (a mixture of CT and HT) inhibited CH_4 production in sheep by 10% and in cattle by up to 30% (Carulla et al., 2005; Grainger et al., 2009), but Min et al. (2005a) found that quebracho CT extract included at concentrations of 1 to 2 mg/mL decreased CH_4 production by 12.3% to 32.6% in vitro.

Goel and Makkar (2012) have noted that the anti-methanogenic effect of tannin-rich diets depends on both the tannin concentration and the number of hydroxyl groups present in the tannin structure. Pellikaan et al. (2011a, b) reported that in vitro ruminal gas and CH_4 production were highly related to the specific chemical structure of tannins, such as type of tannins (i.e., CT vs. HT), solubility, and cis–trans configuration. Several earlier studies have noted that procyanidin (PC) and prodelphinidin (PD)-types of CT may disrupt methanogenesis (Min et al., 2015a; Naumann et al., 2018).

Hydrolysable tannins (e.g., gallic acid subunits) directly constrain methanogens, but the action of CT on rumen CH_4 production is variable (Goel and Markkar, 2012; Aboagye and Beauchemin, 2019). A meta-analysis from 30 experiments comprising 171 treatments showed a linear decrease in both in vitro ($R^2 = 0.69$; $n = 91$) and in vivo ($R^2 = 0.47$; $n = 39$) in CH_4 production with increasing tannin concentrations (Jayanegara et al., 2012). However, some of the CH_4 decrease was due to the concomitant decline of in vivo digestibility ($R^2 = 0.29$) of organic matter (Jayanegara et al., 2012). Min et al. (2015a) reported that reduction rates of ruminal in vitro gas and CH_4 emissions were greater in chestnut (mainly HT; gallic acids) and mimosa (black wattle; mainly catechol) tannins than in quebracho (mainly CT). This difference was probably due to greater sensitivities of some microbial species to these compounds and/or different affinities with other dietary components (e.g., binding capacity with protein) (Haslam, 1989; Hagerman et al., 1992). Wolin (1979) reported that more H_2 and CH_4 were produced during fermentation of fiber than starch, which related to greater propionate synthesis in starch-based diets than fiber fermentation. Vasta et al. (2019) and Min and Solaiman (2018) hypothesized that plant tannins could directly inhibit CH_4 production through decreased methanogenesis pathways and reduced activities of selected rumen microbes (such as cellulolytic bacteria and protozoa) that modify conversion of substrate to H_2 and acetates. Dietary fiber performs to interact with tannins through hydrogen bonds formed with free phenolic groups (Silanikove et al., 2001). Any reduction in dietary fiber digestibility is likely to reduce CH_4 production because fibrolysis provides H_2 as a substrate for methanogenesis in forming acetate from pyruvate (Moss et al., 2000; Tavendale et al., 2005). Therefore, plant tannins could be a useful tool for mitigation of enteric GHG emissions as a potential anti-methanogenic agent. Further research is needed to

assure a sustainable supply of abundant and safe food and other livestock products, whereas reducing emissions of GHG.

7. Areas for future research

Comprehensive in vivo research on ruminants is required to assess the applicability of various dietary interventions in reducing enteric CH_4 gas emissions whereas improving ruminant production without negative effects on the animal. In addition, research is needed that will deliver insight on the potential benefits of plant secondary compounds that produce animals with both reduced CH_4 production and increased feed efficiency, and host-gut microbiome interactions associated with enteric CH_4 emissions. Additional large-scale investigations should be carried out to find optimal tannin levels, types, and conditions to reduce GHG emissions in commercial settings.

8. Summary of findings

The potential to beneficially manipulate the rumen microbiome community structure and meet sustainable with reduce GHG emissions of ruminant production systems through an animal selection program for both reduced CH_4 production and increased feed efficiency, and introduction of dietary interventions has recently progressed toward application of new technologies. Animal DMI is the single important predictor of CH_4 production; however, total methanogens, total protozoa populations, and F:B ratio can significantly affect this relationship. The idea that the host animal controls its own microbiota to significant extent shows potential for implementation of effective breeding strategies. The use of relative abundance of microbial genes in the gastrointestinal tract can affect potential CH_4 emissions. Strategies to mitigate GHG emissions from ruminant livestock production can improve animal performance and feed efficiency while help reducing livestock-induced atmospheric GHG emissions that contribute to global warming. One possible strategy to reduce GHG emissions is dietary modifications that include feeding tannin-rich diets to cattle and other ruminants. Properly designed CT-rich diets can reduce GHG emissions as enteric CH_4 production without detrimental impacts on animal production. Therefore, GHG reduction strategies should be established to increase ruminant production efficiency, whereas minimizing losses of CH_4 and volatile organic compounds from animal agriculture.

Conflict of interest

We state that we have no financial or personal relationships with other people or organizations that can improperly influence our work, there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be contributed as influencing the content of this paper.

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