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

Byeng R. Min, Sandra Solaiman, Heidi M. Waldrip, David Parker, Richard W. Todd, David Brauera

United States Department of Agriculture (USDA), Agricultural Research Service (ARS), Bushland, TX, 79012, USA

Tuskegee University, Tuskegee, AL, 36088, USA

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 CH4 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 CH4 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 CH4 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 CH4 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 CH4 production and the influence of ruminant animals on global GHG emissions.

Keywords:
Feed efficiency
Greenhouse gas (GHG) emission
Methanogenesis
Tannin
Ruminant

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 CH4 production. This review is aimed at providing information on the influence of plant tannins on ruminal microbiota, CH4 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 CH4 production in ruminants both in vivo and in vitro.
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., 2010, 2012; Goel and Makkar, 2012; Min and Solaiman, 2018). In vitro studies have shown that tannin-containing diets or tannin extracts usually reduce enteric CH₄ production. In addition, the effects on animal production and efficiency of animal production need to be evaluated. Methods and practices to reduce CH₄ 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 (CO₂) and CH₄ (Johnson and Johnson, 1995; Gerber et al., 2013). Limited studies have considered the relationship between plant tannins and CH₄ emissions per unit of DMI, animal performance, rumen fermentation, and feed efficiency dynamics (Wagahorn and Hegarty, 2011; Beuchemin et al., 2007). This review summarized available literature on the impact of DMI and tannins on CH₄ emissions, rumen fermentation (2012; 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 (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 more animal-friendly application. The most widely used techniques are the indirect recording methods that are based on the principle of estimating CH₄ production 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 (C₆H₁₂O₆) + ammonia (NH₃) → Rumen microbes + CH₄ + CO₂ + 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 H₂ formed; therefore, quantity of CH₄ produced from glucose varies depending on microbial activity and biological reactions (Janssen, 2010). In the rumen, methanogens use H₂ to reduce CO₂ to CH₄ (Van Soest, 1994). In this pathway, which may involve coenzyme M (Miller et al., 1986), 4 mol of H₂ are used to produce CH₄ (Czerkawski, 1986). Formation of butyrate + H₂ or acetate + butyrate + H₂ have been shown to be predominant pathways under low ruminal H₂ concentrations, whereas the accumulation of acetate + propionate was predominant at higher H₂ concentrations (Janssen, 2010). If ruminal VFA production favors less acetate production relative to propionate (i.e., lower A:P ratio), the net equilibrium of H₂ in the rumen decreases and results in reduced CH₄ formation (van Nevel and Demeyer, 1996). Most rumen methanogens attain energy for their growth through a sequence of biological reduction of CO₂ with H₂ (methanogenesis pathway: 4H₂ + CO₂ → CH₄ + 2H₂O), whereas some methanogens use the acetogenesis pathway (CH₃COOH → CH₄ + CO₂) (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 CH₄ emissions in ruminants, which are discussed in the following section, may reduce enteric GHG production and simultaneously improve FCE and profitability.

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 CH₄ 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, 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, CH₄ 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 (H₂) 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 CH₄ emissions (McSweeney and Mackie, 2012). A summary of methanogenesis and microbial fermentation of dietary components in the rumen resulting in the production of VFA, CH₄, CO₂, and H₂ emitted through eructation is presented in Fig. 1. It has been noted that feeding grain-based diet that are high in starch instantly lowered CH₄ emission (g/d and kg DMI); whereas, diets with forage-based diet resulted in increased CH₄ emissions (Fig. 1; Wallace et al., 2014). In ruminants, 87% to 89% of enteric CH₄ 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).
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 CH4 emissions is the SF6 tracer method (Zimmerman, 1993). For this method, a bolus containing SF6 is deposited in the rumen and concentrations of SF6 and CH4 in the breath are analyzed by gas chromatography. The concentration of CH4 is corrected for dilution by external air from the measured SF6 concentration. Results with the SF6 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 CH4 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 CH4 concentrations and the low background concentration in the atmosphere (Crowcon, 2014). However, there was not a strong relationship LMD and the dynamics of CH4 concentrations exhaled by ruminants (Chagunda, 2013) and dairy wastewater (Todd et al., 2011). When it is used to study the CH4 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 CH4 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 CH4 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 CH4 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 CH4 emissions from cattle.

5.1. Dry matter intake and methane emissions

When the regression analysis was conducted using the data in Table 1, CH4 production was strongly correlated with DMI as described by Eq. (1).

\[ \text{CH}_4(\text{g/d}) = 20.53 \times \text{DMI(\text{kg/d})} + 24.62 \left( R^2 = 0.82; P < 0.001 \right) \]

Eq. (1)

Each 1.0-kg increase in DMI increased CH4 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 CH4-measurement methods (IRC, SF6, and GF). The slope of the proposed general relationship between CH4 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 (CH4 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.

| Reference                  | Animal breed | BW, kg/animal | Ration type | DMI, kg/d per animal | CH4, 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          | SF6            |
|                            |              |               | low-RFI     | 9.33                 | 20.3          | SF6            |
| 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 + WDGS | 5.2               | 12.88         | IRC            |
|                            |              |               | beef TMR     | 5.2                  | 12.83         | IRC            |
| Hammond et al. (2015)       | heifer       | 317 to 339    | grazing     |                      |               |                |
|                            |              |               | period I    | 7.62                 | 26.6          | GF             |
|                            |              |               | period II   | 7.66                 | 28.3          | IRC            |
|                            |              |               | period III  | 7.54                 | 27.7          | IRC            |
|                            |              |               | period IV   | 9.15                 | 18.8          | GF             |
|                            |              |               | period V    | 9.15                 | 21.5          | SF6            |
|                            |              |               | period VI   | 10.0                 | 17.3          | GF             |
|                            |              |               | period VII  | 8.13                 | 28.4          | IRC            |
|                            |              |               | period VIII | 10.0                 | 21.8          | SF6            |
|                            |              |               | RC          | 6.86                 | 29.5          | GF             |
|                            |              |               | BT          | 7.93                 | 28.9          | GF             |
|                            |              |               | wild flowers | 7.4                 | 27.8          | GF             |
|                            |              |               | alfalfa     | 7.42                 | 25.7          | IRC            |
|                            |              |               | alfalfa     | 8.78                 | 19.7          | GF             |
|                            |              |               | alfalfa     | 8.78                 | 19.5          | SF6            |
| Herd et al. (2016)          | heifer       | 317 to 339    | ryegrass    | 10.0                 | 21.8          | GF             |
|                            |              |               | RC          | 8.69                 | 23.0          | SF6            |
|                            |              |               | wild flowers | 8.78                 | 19.5          | SF6            |
| Jonker et al. (2016)        | Hereford/Friesian heifer | 382        | alfalfa silage-based | 7.4          | 15.0          | GF             |
| McGaughey et al. (1997)     | steer        | 356.2         | rotational stocking | 7.6          | 19.0          | GF             |
|                            |              |               | HSR         | 14.94                | 17.65         | IRC            |
|                            |              |               | LSR         | 13.61                | 20.85         |                |
|                            |              |               | continuous stocking | 13.51        | 17.92         |                |
| McGinn et al. (2009)        | steer        | 381.2         | barley grains (35%) | 9.5          | 23.8          | SF6            |
|                            |              |               | corn DDGS (35%) | 9.0          | 19.9          |                |
| Pedreira et al. (2013)      | steer        | 444.3         | with no concentrate, 100% SS | 5.52        | 22.76         | SF6            |
|                            |              |               | with 30% concentrate + 70% SS | 7.9          | 18.87         |                |
|                            |              |               | with 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 | 47:53       | 18.2          | IRC            |
|                            |              |               |              | 54:46                 | 25.9          |                |
|                            |              |               |              | 61:39                 | 28.2          |                |
|                            |              |               |              | 68:32                 | 29.1          |                |
| Arbe et al. (2016)          | dairy cow    | 723 to 729    | 60% hay + 40% grains silage-based diet | 9.7          | 23.6          | SF6            |
|                            |              |               |              | 23.8                  | 17.4          | GF              |
daily CH4 production by cattle based solely on their DMI when no steers or non-lactating heifers with lower DMI and low CH4 measurements in the beef dataset were from growing/finishing. Therefore, it makes direct comparisons more difficult because the DMI ranges are varied between dairy and beef cattle. It is environment. However, Eq. (1), based on the data from Table 1 and 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 CH4 production values. Measurements in the dairy dataset were from lactating Holstein-Friesian dairy cows with a high DMI and high CH4 production, whereas measurements in the beef dataset were from growing/finishing steers or non-lactating heifers with lower DMI and low CH4 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 environments. However, Eq. (1), based on the data from Table 1 and presented in Fig. 2B, provides a rather simple means to estimate daily CH4 production by cattle based solely on their DMI when no other information is available. An R² of 82% implied that DMI strongly influenced CH4 production. Since most dairies and feedlots know their cattle’s DMI, an inventory of CH4 emission is possible.

Most national inventories assume CH4 production is linear with DMI (Hristov et al., 2013b; Miller et al., 2013; Niu et al., 2018). This assumes that CH4 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 CH4 production values from beef cattle studies using different CH4-measurement methods, cattle breeds, diets, and geographic location are so diverse that a universal CH4 production value may not be recommended at this stage. This agrees with our current study which indicated that the 3 different CH4-measurement methods (IRC, SF6, and GF) may misrepresent the relationship between daily CH4 production and DMI (g/kg DMI; Fig. 2A). Based on the present study, average estimate of CH4 production (g/d) varied among the 3 measurement techniques, mean (±SE) values were 39.8 ± 3.5 (beef-SF6), and 17.2 ± 2.2 (dairy-SF6) for dairy cattle. Overall CH4 emissions determined using GF and SF6 were significantly lower (P < 0.05) than those measured using IRC technique. Differences in daily CH4 production between GF and other techniques are likely due to the short duration of the CH4 measurements obtained for

| Reference                | Animal breed | BW, kg/animal | Ration type                | DMI, kg/d per animal | CH4, g/kg DMI | Technique used |
|--------------------------|--------------|---------------|----------------------------|---------------------|---------------|---------------|
| Bharanidharan et al. (2018) | Holstein     | 540.3         | TMR                        | 12.3                | 11.3          | IRC           |
| Dini et al. (2012)       | Holstein     | 536.2         | roughage, concentrate      | 10.2                | 10.3          | SF6           |
| Hammond et al. (2014)    | Holstein/Friesian | 339.8   | legume-dominated           | 17.3                | 29.4          | SF6           |
| Hristov et al. (2015)    | Dairy cow    | 653           | control (n = 7)            | 26.7                | 20.4          | GF            |
| Grainger et al. (2007)   | Holstein/Friesian | 496.6   | rye grass                  | 8.03                | 28.4          | SF6           |
| Lee et al. (2004a)       | Holstein/Friesian | 496.6   | rye grass with no WC       | 15.6                | 21.7          | SF6           |
| Odongo et al. (2006)     | Holstein cow  | 620.6         | TMR + 24 mg Rumensin       | 19.7                | 23.3          | IRC           |
| Olijhoek et al. (2017)   | Jersey       | 647.6         | high-RFI/low-concentrate   | 30.7                |               | IRC           |
| Rischewski et al. (2017) | Holstein     | 655           | period I                   | 16.9                | 20.0          | GF            |
| Wims et al. (2010)       | Holstein/Friesian | 493.8   | period II                  | 20.6                | 18.4          | SF6           |
| Woodward et al. (2002)   | Friesian/Jersey | 538    | period III                 | 20.7                |               |               |
| Woodward et al. (2004)   | Friesian     | 538           | period III                 | 19.3                |               | SF6           |
| Waghorn et al. (2016)    | Holstein/Friesian | 520    | LSR (n = 4 periods)        | 21.8                |               | GF            |

DMI – dry matter intake; RFI – residual feed intake; GF – GreenFeed system (C-Lock Inc., Rapid City, SD, USA); IRC – indirect respiratory chamber; SF6 – sulfur hexafluoride tracer technique; TMR – total mixed ration; WDGS – wet distiller’s grains with solubles; DDGS – dry distiller’s grains with solubles; SS – sorghum silage; RC – red clover (Trifolium pratense); BT – birdfoot 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 CH4 emissions per DMI is presented in Fig. 2.
2 Dry matter intake and CH4 yield were used to calculate daily CH4 emissions. Animals of different ages and BW were used in the dairy and beef data sets, with correspondingly different DMI and CH4 production values.
3 Wild flowers are mixtures of a rye grass (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 LSRe and HSR means low- and high-stocking rates.
each animal (Hammond et al., 2015). The variation in DMI for beef cattle with the GF was much smaller than the variation in measured CH4 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

![Figure 2](image-url)

**Fig. 2.** Selected studies of methane emissions from widely used techniques. (A) Effects of dry matter intake (DMI) on daily CH4 emissions in dairy and beef cattle associated with detection methods, and (B) effects of DMI on average daily CH4 emissions in dairy and beef cattle. SF6 = sulfur hexafluoride tracer technique; IRC = indirect respiration chamber; GF = GreenFeed system (C-Lock Inc., Rapid City, SD, USA). Source: adapted from Table 1.
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 SF6 breath measurement systems is that the amount of CH4 production from the hind gut be measured with GF and SF6 (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 CH4 emissions. Two explanations for lower values of GF and SF6 are possible: 1) CH4 production by the hindgut is much greater impact; 2) CH4 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 CH4-measurement techniques, cumulative daily CH4 production may be under- or over-estimated because of diurnal patterns in CH4 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 CH4 production, and 2) the average rate of CH4 production is between 15 and 25 g per kg of DMI.

5.2. Feed conversion efficiency and CH4 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 and Tedeschi, 2006). 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 measurement 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 CH4 emissions in beef and dairy cattle is weak (Waghorn and Hegarty, 2011). Hegarty et al. (2007) reported a significant relationship between CH4 emission and RFI for Angus steers. However, RFI accounted for only a small proportion of the variations in CH4 production. The data suggest that animal selection could only reduce CH4 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 CH4 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 CH4 as a function low-RFI (<0; more efficient) and high-RFI (>0; less efficient) beef cattle. These findings demonstrate that differences in CH4 production may not be directly associated with RFI, but rather they are due to RFI-induced differences in DMI (Fre et al., 2015). However, several studies have shown a positive relationship between RFI and CH4 production but the effect of RFI on CH4 is not consistent across all studies (Fre et al. and Brown-Brändi, 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 CH4 production, which is small. However, there are several physiological mechanisms, which have no effect on CH4 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 CH4 production. Waghorn and Hegarty (2011) reported no differences in CH4 emissions because of higher FCE, resulting in lower energy losses as CH4. However, such a strategy has yet to be evaluated.

### Table 2

| Item          | Average | 10% higher ADG | 10% higher FCE |
|---------------|---------|----------------|----------------|
| 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, $ | 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

| 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 | 0.66 ± 0.05 |
| NFE or RFI | − | − | 0.39 ± 0.03 |

ADG = average daily gain; BW = body weight; DMI = dry matter intake; FCE = feed conversion efficiency (feed efficiency 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.
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 CH₄ production did not differ between heifers with high- and low-RFI. When adjusted for DMI, CH₄ 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 CH₄ emission per day or CH₄ emission per kilogram BW in dairy heifers; however CH₄ 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 methanogenic 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 Methanospirillum 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 CH₄ 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 CH₄ emissions than those fed a forage-based diet (Wallace et al., 2014; Roche 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 H₂ available for typical CH₄ producing pathway (Beauchemin and McGinn, 2005; Cottle and Eckard, 2018). Thus, CH₄ reduction strategies that reduce available H₂ 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 H₂-using pathway; therefore, acetogens may function as a net H₂ sink that reduces CH₄ emissions (van Nevel and Demeyer, 1996). However, the primary cellulolytic bacterial species and protozoa in the rumen are H₂ producing microbes; thus, counteracting CH₄ reduction strategies that reduce available H₂ may slow cellulose digestion (Latham and Wolin, 1977; Ungerfeld, 2015).

The number of methanogenic archaea may not be a strong determinant of CH₄ 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 CH₄ 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 CH₄ production and the concentration of methanogens in the rumen. A positive correlation between CH₄ 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 CH₄ emissions (g/d) in sheep and goats. In addition, CH₄ 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 CH₄ production, and the relative abundance of M. ruminantium and low CH₄ production, have been reported (Shi et al., 2014; Danielsson et al., 2017) in sheep and dairy cattle.
A possible explanation for this could be competition for the same substrate, as *Methanobrevibacter* species are hydrogenotrophs (Leahy et al., 2013) and use H₂ and/or formates as substrates for CH₄ production. Therefore, different methanogenic species could have an advantage at different H₂ concentrations and/or respond differently (because of different methanogenic enzymes; Reeve et al., 1997) to produce CH₄ (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 CH₄ production and can potentially be utilized to estimate CH₄ 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 CH₄ production. These same authors stated that Firmicutes populations were linked to lower VFA levels when CH₄ 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 CH₄ 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 CH₄ emissions, but host microbiome cross talk genes (e.g., GDP-α-fucose synthetase [TSTA3] and α-fucose isomerase [Fucl]) were related to FCE. Published data also showed that higher rumen particulate passage was linked with lower rumen H₂ concentrations, reduced CH₄ 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 CH₄ production per unit of DMI per day.

### 5.5. Other strategies for methane emissions

Several potential enteric CH₄ mitigation strategies (Fig. 5) have been proposed, including use of CH₄ 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 CH₄ oxidation, improvements in forage quality, and genetic selection of low CH₄ producing ruminants (Beauchemin et al., 2008; Hristov et al., 2013a, b). Ionophores have not been...
proposed but have been used for more than 40 years commercially. The most effective strategy for reducing \( \text{CH}_4 \) emissions will likely incorporate several of these mitigation strategies (Beauchemin et al., 2008). These approaches have emerged as means to decrease \( \text{CH}_4 \) 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, \( \text{CH}_4 \) 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 to decrease \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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 \( \text{CH}_4 \) emissions of varying tannin-rich diets (e.g., Sericea lespedeza) in both in vitro and in vivo settings. The relationship between CT (% DMI) and reduces \( \text{CH}_4 \) production per unit of DMI (Fig. 6) indicated that increasing CT in the diets linearly reduced \( \text{CH}_4 \) 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 \( \text{CH}_4 \) 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), CH4 emissions were decreased by 13%. Grainger et al. (2009) reported that CH4 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 CH4 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 bihydrogenation of fatty acids, suggesting that CT in diets may produce potentially value-added milk in the future (Khiao-Ard et al., 2015).

Dairy cows fed diets composed of CT-rich birdsfoot trefoil silage or perennial ryegrass (Lotium perenne) silage had similar total CH4 emissions, but total CH4 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 CH4 production of 24.6 g/kg DMI when dairy cows were grazing perennial ryegrass pasture, compared to CH4 (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. 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), Patza et al. (2017), Roeche et al. (2016), Ross et al. (2013), Tavendale et al. (2005), and Woodward et al. (2001).
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 CH4 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 CH4 production was reduced by 25% to 51% (Min et al., 2005a, 2006b). It appears that a CT-rich diet can effectively decrease CH4 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 CH4 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 CH4 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 CH₄ 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 CH₄ production was decreased at a rate of 1.2 mol of CH₄ per mole of catechin (Becker et al., 2014).

Dominant ruminal cellulolytic bacterial species, including Fibrobacter succinogenes, Ruminococcus albus, and Ruminococcus flavefaciens (Koike and Kobayashi, 2009), may influence CH₄ production (Chauveyras-Durand et al., 2010). Min et al. (2006a) reported that cultures from R. albus and R. flavefaciens produced the most H₂ among dominant ruminal cellulolytic bacterial strains. In addition, these cellulolytic bacteria resulted in greater CH₄ production when cultured with M. smithii compared with other co-cultured combinations. More recent research indicated that tannin-rich diets resulted in ruminal CH₄ suppression through reduced methanogen population size (Min et al., 2014a, b; Christensen et al., 2017) and decreased H₂ 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 B) 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 CH₄ production; higher concentrations of propionate and lower concentrations of acetate have been found to reduce CH₄ emissions (Monteny et al., 2006). Rumen A:P ratio may also be associated with a lower CH₄ production per unit of DMI in ruminants. As ruminal VFA production changes towards less production of acetate relative to propionate (i.e., lower A:P ratio), the net concentrations of H₂ in the rumen decreased via physical intracellular hydrogenosomes, resulting in less CH₄ 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 CH₄-producing archaea and some cellulolytic bacteria (R. flavefaciens) (Bhatta et al., 2009). Ruminal fungi and protozoa have been linked to CH₄ formation (Khiaosa-Ard et al., 2015). The process of protozoal CH₄ formation is via hydrogenosomes. This protozoa-derived H₂ was associated with methanogens in the rumen (Mosoni et al., 2011). To enhance access to H₂, 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 CH₄ from ruminants is produced by protozoa-associated methanogens (Finlay et al., 1994). Tymensen et al. (2012) confirmed that numbers of Methanobrevibacter 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 CH₄ 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., 2015b). Inclusion of wattle tannin extracts (a mixture of CT and HT) inhibited CH₄ 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/µL decreased CH₄ production 12.3% to 32.6% in vitro.

Goel and Malkar (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 CH₄ 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 CH₄ 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 (R² = 0.69; n = 91) and in vivo (R² = 0.47; n = 39) in CH₄ production with increasing tannin concentrations (Jayanegara et al., 2012). However, some of the CH₄ decrease was due to the concomitant decline of in vivo digestibility (R² = 0.29) of organic matter (Jayanegara et al., 2012). Min et al. (2015a) reported that reduction rates of ruminal in vitro gas and CH₄ 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 H₂ and CH₄ 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 CH₄ production through decreased methanogenesis pathways and reduced activities of selected rumen microbes (such as cellulolytic bacteria and protozoa) that modify conversion of substrate to H₂ 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 CH₄ production because fibrosilysis provides H₂ 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 CH₄ 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 CH₄ production and increased feed efficiency, and host-gut microbiome interactions associated with enteric CH₄ 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 CH₄ production and 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 CH₄ 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 CR-rich diets can reduce GHG emissions as enteric CH₄ production without detrimental impacts on animal production. Therefore, GHG reduction strategies should be established to increase ruminant production efficiency, whereas minimizing losses of CH₄ 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.

References

Aboagye IA, Beauchemin KA. Potential of molecular weight and structure of tannins to reduce methane emissions from ruminants: a review. Animals 2019;9(856): 1–18.
Aguerre MJ, Wattiaux MA, Powell JM, Broderic GA, Arndt C. Effect of forage-to-concentrate ratio in dairy cow diets on emission of methane, carbon dioxide, ammonia, lactation performance, and manure excretion. J Dairy Sci 2011;94: 3081–93.
Alenu AW, Vyas D, Manafzavar G, Basarab JA, Beauchemin KA. Enteric methane emissions from low- and high-residual feed intake beef feeders measured using GreenFeed and respiration chamber techniques. J Anim Sci 2017;95: 3727–37.
Alexandratos N, Bruinsma J. World agriculture towards 2030/2050: the 2012 revision. FAO, Food and Agriculture Organization of the United Nations; 2012.
Animit G, Puchala R, Goetsch AL, Patra AK, Sahu T, Varel VH, Wells J. Methane emission by goats consuming diets with different levels of condensed tannins from Sespedesia. Anim Feed Sci Technol 2010a:144:212–27.
Animit G, Puchala R, Goetsch AL, Patra AK, Sahu T, Varel VH, Wells J. Methane emission by goats consuming different source of condensed tannins. Anim Feed Sci Technol 2000b:144:228–41.
Arleve M, Rochette Y, Gayader J, Lasousc C, Gomez LM, Eugene M, Morgav DP, Renand G, Doreau M, Martin C. Repeatability of enteric methane determinations from cattle using either the SF6 tracer technique or the GreenFeed system. Anim Prod Sci 2016;56:238–45.
Arthur PF, Archer JA, Johnston DJ, Herring RL, Richardson EC, Parnell PF. Genetic and phenotypic variance and covariance components for feed intake, feed efficiency and other postweaning traits in Angus cattle. J Anim Sci 2001;79:2805–11.
Attwood C, McSweeney C. Methanogenics genomics to discover targets for methane mitigation technologies and options for alternative H₂ utilization in the rumen. Aust J Exp Agric 2008;48:28–37.
AustDist DE, Atkinson KL, Silvapulle MJ, Dellow DW, McDowell GW. Utilization of white clover silage fed alone or with maize silage by lactating dairy cows. Aust J Exp Agric 1999;39:237–46.
Bae HD, McAllister TA, Yanke J, Cheng KJ, Muir AD. Effects of condensed tannins on endoglucanase activity and filter paper digestion by Fibrobacter succinogenes SBS. Appl Environ Microbiol 1993;59:2311–6.
Basarab JA, Price MA, Altshull JL, Okine EK, Shelling WM, Lyle KL. Residual feed intake and body composition in young growing cattle. Can J Anim Sci 2003:83:189–204.
Basarab JA, Beauchemin KA, Baron VS, Ominsky KH, Cuan LL, Miller SP, Crowley JJ. Reducing GHG emissions through genetic improvement for feed efficiency: effects on economically important traits and enteric methane production. Anim 2013;7:303–3015.
Beauchemin KA, McGinn SM. Methane emissions from feedlot cattle fed barley or corn diets. J Anim Sci 2005;83:653–61.
Beauchemin KA, McGinn SM. Enteric methane emissions from growing beef cattle as affected by diet and level of intake. Can J Anim Sci 2006;86:401–8.
Beauchemin KA, McGinn SM, Martinez TF, McAllister TA. Use of condensed tannin extract from quebracho trees to reduce methane emissions from cattle. Can J Animal Sci 2007;85:1990–6.
Beauchemin KA, Kreuzer M, O’Mara F, McAllister TA. Nutritional management for enteric methane abatement: a review. Aust J Exp Agric 2008;48:21–7.
Becquer PM, Wiksaelaar PG, Franssen MCR, Vos BCH, Hall RD, Beekwelder J. Evidence for a hydrogen-sink mechanism of (+)-catechin-mediated emission reduction of the ruminant greenhouse gas methane. Metabolomics 2014;10:179–89.
Bhurathanaran R, Arakyakoon GS, Kim ER, Lee CH, Yang W, Kim NY, Kim KM. Ruminal methane emissions, metabolic, and microbial profile of Holstein steers fed forage and concentrate, separately or as a total mixed ration. PLoS One 2018;13:19.
Bhatta R, Uyenoy TJ, Tajima K, Takenaka A, Yabumoto Y, Nonaka I, Enishi O, Kurihara M. Difference in the nature of tannins on in vitro ruminal methane and volatile fatty acid production and on methanogenic archaea and protozoal populations. J Dairy Sci 2009;92:5312–22.
Broucke JS. Options to methane production abatement in ruminants: a review. J Anim Plant Sci 2011;7:394–8.
Buchanan RW, Gilbert RJ. Selective feeding of cattle increases enteric methane and urinary nitrogen in forage-fed sheep. J Anim Sci Biotechnol 2014;5:1–5.
Carrasco JM, Cabral DC, Redondo LM, Visco NDP, Miyakawa MEF. Impact of chestnut and quebracho tannins on rumen microbiota of bovines. BioMed Res Int 2017:1–12.
Carstens GE. Net feed intake: potential selection tool to improve feed efficiency in beef cattle. 2019. www.agribsa.co.za/Documents/BreeplanTraits/Texas AandM.pdf. [Accessed 11 April 2019].
Carstens GE, Tedesco LD. Defining feed efficiency in beef cattle. April 18-21. In: Beef improvement federation conference. Chotch, MUS; USA: 2006. p. 12–21.
Carulla JE, Kreuzer M, Machmuller A, Hess HD. Supplementary of Acacia mearnsii tannins decreases methanogenesis and urinary nitrogen in forage-fed sheep. J Anim Sci Biotechnol 2014;5:1–5.
Changanda MG, Ung C, White L, Starcher SE, Gribble T, Gribble JS. A single equation to predict methane production of forage-fed beef cattle in Australia. Anim Prod Sci 2017;56:169–80.
Chaudhury-Durand F, Massigella S, Fonty G, Forano E. Influence of the composition of the cellulosic flora on the development of hydrogenotrophic microorganism, hydrogen utilization, and methane production in the rumens of ruminobiotically reared lambs. Appl Environ Microbiol 2010;76:7931–7.
Chen S, Cheng H, Wyckoff KN, He Q. Linkages of Firmicutes and Bacteroidetes populations to methanogenic process performance. J Int Micro Biotech 2017;43:771–81.
Chiquette J, Cheng KJ, Costerton JW, Milgrom LP. Effect of tannins on the digestibility of two isosynthetic strains of birdsfoot trefoil (Lotus corniculatus L.) using in vitro and in sacco techniques. Can J Anim Sci 1988;68:751–60.
Christensen RG, Eun JS, Yang YS, Min BR, MacAdams JW. In vitro effects of birdsfoot trefoil (Lotus corniculatus L.) pasture on ruminal fermentation, microbial population and methane production. Prof Anim Sci 2017;33:451–60.
Clark H, Pinares-Patino CS, de Klein CAM. Methane and nitrous oxide emissions from grazed grasslands. In: McGuilloway DA, editor. Grassland: a global resource. Wageningen (The Netherlands): Wageningen Academic; 2005. p. 279–92.

Cottle DJ, Eckard RJ. Global beef cattle methane emissions: yield prediction by cluster and meta-analyses. Anim Prod Sci 2018;58:2167–77.

Crowcon. Monitoring and analysis of landfill gases. 2014. www.crowcon.com/blog/monitoring-landfillgases. [Accessed 24 May 2019].

Czerkawski J. An introduction to rumen studies. Oxford, New York, Toronto, Sydney, Frankfurt: Pergamon Press; 1986.

Danielsson R, Schuurman A, Artursson V, Bertilsson J. Methanogenic population and CH4 production in dairy cows fed different levels of forage. Eur Environ Microbiol 2012;78:6172–9.

Danielsson R, Dicksev J, Sun L, Gonda H, Muller B, Schuurman A, Bertilsson J. Methane production in dairy cows correlates with rumen methanogenic and bacterial communities. Front Microbiol 2016;7:1–15.

Deighton MH, Williams SRO, Hannah MC, Eckard RJ, Boland TM, Wales WJ, Moate PJ. A modified sulphur hexafluoride tracer technique enables accurate determination of enteric methane emissions from ruminants. Anim Feed Sci Technol 2014;197:47–63.

Dewhurst RJ, Evans RT, Scolan ND, Morry MJ, Merritt RJ, Wilkinson JJ. Comparison of grass and legume silages for milk production. I. Production responses with different levels of concentrate. J Dairy Sci 2003;86:2598–611.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.

Dijkstra J, Zijderveld SM, van Apajalahti JA, Bannink A, Gerrits WJJ, Newbold JR, Hammond KJ, Jones AK, Humphries DJ, Crompton LA, Reynolds CK. Effects of diet and concentrate type on methane emissions from animal operations: I. A review of enteric methane mitigation options. J Anim Sci 2013a:91:5045–69.
carcass traits in steers fed a high-grain diet. Anim Feed Sci Technol 2010;159:1–9.

Larsen NJ. Performance and methane emissions of RFI selected cattle in dairying and under open range conditions. M.Sc. Thesis. Rangeland Research Institute, University of Alberta; 2018.

Lassey RR, Ulltay MJ, Martin RJ, Walker CF, Shelton JD. Methane emissions measured directly from grazing livestock in New Zealand. Atmos Environ 1997;31:2905–14.

Latham MJ, Wolin MJ. Fermentation of cellulose by Ruminococcus flavefaciens in the presence and absence of Methanobacterium ruminantium. Appl Environ Microbiol 1997;63:297–303.

Leahy SW, Kelly R, Ronimus N, Wedlock E, Alterman A, Attwood GT. Genome sequencing of rumen bacteria and archaea and its application to methanogenesis. Anim 2013;7:235–45.

Lee JM, Woolard SL, Attwood GT, Clark DA. Methane emissions by dairy cows fed increasing proportions of white clover (Trifolium repens) in pasture. Proc NZ Grass Assoc 2004;66:151–5.

Liu Y, Whitman WB. Dynamic, phylogenetic, and ecological diversity of the methanogenic archaea. Anna NY Aca Sci 2008;1125:171–89.

Liu H, Vaddella V, Zhou D. Effects of chestnut tannins and coconut oil on growth performance, methane emission, ruminal fermentation, and microbial populations in sheep. J Dairy Sci 2011;94:6069–77.

McCaughhey K, Wittenberg K, Corrigan D. Methane production by steers on pasture. Can J Anim Sci 1997;77:519–24.

McDonnell RP, Hart JK, Boland TM, Kelly AK, McGee M, Kenny DA. Effect of divergent in phenotypic residual feed intake on methane emissions, ruminal fermentation, and rumen volatile short chain fatty acid levels in Holstein heifers across three contrasting diets. J Anim Sci 2016;94:303–15.

McCinn SM, Chung YH, Beauchemin KA, Iwaasa AD, Grainger C. Use of corn distillers’ dried grains to reduce enteric methane loss from beef cattle. Can J Anim Sci 2009;89:409–13.

McNabb WC, Waghorn GC, Peters JS, Barry TN. The effect of condensed tannins in Lotus pedunculatus on the solubilization and degradation of ribulose-1,5-bisphosphate carboxylase (EC 4.1.1.39; RuBisCO) protein in the rumen and the sites of RuBisCO digestion. Br J Nutr 1996;76:535–54.

McSweeney CS, Mackie R. Micro-organisms and ruminate digestion: state of knowledge, trends and future prospects, Commission on Genetic Resources for Food and Agriculture. Background Study 2012;63:1–66.

Mercadante MEZ, Caliandro APDM, Canesin RC, Bonilha SFM, Berndt A, Frigotto RT, Branco RH. Relationship between residual feed intake and enteric methane emission in Nellore cattle. Rev Bras Zoot 2015;44:255–62.

Miller TL, Wolin M, Atkinson MR. Characteristics of methanogens isolated from the bovine rumen. Appl Environ Microbiol 1986;51:201–2.

Miller SM, Steven C, Michalak AM, Kort EA, Andrews AE, Biaudet SC, et al. Anthropogenic emissions of methane in the United States. Proc Natl Acad Sci U S A 2013;110:200–22.

Min BR, Hart SP. Tannins for suppression of internal parasites. J Anim Sci 2003;81:E102–9.

Min BR, Solarina S. Comparative aspects of plant tannins on digestive physiology, nutrition and microbial changes in sheep and goats: a review. J Anim Physiol Anim Nutr 2018;2018:1–13.

Min BR, Barry TN, Attwood GT, McNabb WC. The effect of condensed tannins on the nutrition and health of ruminants fed fresh temperate forages: a review. Anim Feed Sci Technol 2010;159:263–12.

Min BR, Pinchak WE, Anderson RC, Puchala R. Mitigation potential of condensed tannins in Lotus pedunculatus and Lotus corniculatus on the growth efficiency of proteolytic rumen bacteria in vitro and their possible mode of action. Can J Microbiol 2001;47:626–33.

Monteny GJ, Bannink A, Chadowick D. Greenhouse gas abatement strategies for animal husbandry. Agric Ecosyst Envir 2006;112:163–70.

Morgavi DP, Forano E, Martino CL, Molano AL. Microbial ecosystem and methanogenesis in ruminants. Animal 2010;4:1024–36.

Mosoni P, Martin C, Forano E, Morgavi DP. Long-term defaunation increases the abundance of cellulolytic ruminococci and methanogens but does not affect the bacterial and methanogen diversity in the rumen of sheep. J Anim Sci 2011;89:783–7.

Moss AR, Jouan JP, Newbold J. Methane production by ruminants: its contribution to global warming. Anim Res 2009;49:231–53.

Murray RM, Bryant AM, Molan AL, Barry TN. Effect of methanogenesis of methane in the rumen and large intestine in sheep. Br J Nutr 1976;36:1–14.

Murray RM, Bryant AM, Leng RA. Methane production in the rumen and lower gut of sheep given lucerne chaff: effect of level of intake. Br J Nutr 1978;39:37–45.

Myer PR, Smith TPL, Wells JE, Kuehn LA. Freely Herd. Rumen microbiome from steers differing in feed efficiency. PloS One 2015;10:1–17.

Myer PR, Freely HC, Wells JE, Smith TPL, Kuehn LA. Analysis of the gut bacterial communities in beef cattle and their association with feed intake, growth, and efficiency. J Anim Sci 2017;95:2315–24.

Nagaraja TG, Newbold CJ, van Nevel CJ, Demeyer DI. Manipulation of ruminal fermentation. In: Hobson PN, Stewart CS, editors. The rumen microbial ecosystem. 2nd Eds. London, UK: Blackie Academic and Professional, 1997.

Nakamura N, Lin HC, McSweeney CS, Mackie RI, Gaskins HR. Mechanisms of microbial hydrolysis in the human colon and implications for health and disease. Annu Rev Food Sci Technol 2010;1:363–92.

Naumann H, Sepela R, Rezaire A, Masih SE, Zeller WE, Reinhardt LA, Robe JT, Sullivan MJ, Hagerman AE. Relationships between structures of condensed tannins from Texas legumes and methane production during in vitro rumen digestion. Molecules 2018;23:1–16.

Niu M, Keerabah E, Hristov A, Oh JP. Prediction of enteric methane production, and intensity in dairy cattle using an intercontinental database. Global Change Biol 2018;24:3368–89.

Nikrouzinejad DK, Okine EK, Matheson GW, Schindl K, Li C, Rasbaraj A, Price MA, Wang Z, Moore SS. Relationships of feedlot feed efficiency, performance, and feeding behavior with metabolic rate, methane production, and energy partitioning in beef cattle. J Anim Sci 2006;84:145–53.

Ondy G, Rebbig R, Vess GA, Dick P, Go-Rashid MM, Hook SE, Gray JT, Kebreab E, France J, Mcbride BW. Long-term effects of feeding monensin on methane production in lactating dairy cows. J Dairy Sci 2006;90:1781–8.

Oolhoek DW, Lovendahl P, Lassen J, Helgwing ALF, Hodgikyn JG, Wessberg MJ, Noel SJ, McLean F, Lund P. Methane production, rumen fermentation, and diet digestibility of Holstein and Jersey dairy cows being divergent in residual feed intake and fed at two feed-to-concentration ratios. J Dairy Sci 2017;101:9926–40.

Owens FN, Hanson FC. Symposium: external and internal markers, external and internal markers for appraising site and extent of digestion in ruminants. J Dairy Sci 1992;75:2605–17.

Palmonari A, Stevenson DM, Mertens DR, Cruywagen CW, Weiner PJ. pH dynamics and bacterial community composition in the rumen of lactating dairy cows. J Dairy Sci 2011;94:834–42.

Patra AK. Enteric methane mitigation technologies for ruminant livestock: a synthesis of current research and future directions. Environ Monit Assess 2012;175:19–29.

Patra AK. Recent advances in measurement and dietary mitigation of enteric methane emissions in ruminants. Front Vet Sci 2016;3:1–17.

Patra A, Park T, Kim M, Yu Z. Rumen methanogens and mitigation of methane emission by anti-ethanogenic compounds and substances. J Anim Bio- techol 2017:8;1–18.

Pedreira MS, Oliveira SG, Primavesi O, Lima MA, Frigotto RT, Berchielli TT. Methane emissions and estimates of ruminal fermentation parameters in beef cattle fed different dietary concentrate levels. Rev Bras Zootec 2013;42:592–600.

Pekkanen WF, Hendriks WH, Uwimana G, Bongers LJCM, Becker PM, Cone JW. A novel method to determine simultaneously methane production during the in vitro gas production using a fully automated equipment. Anim Feed Sci Technol 2011a;168:118–30.

Pekkanen WF, Stringano E, Leenaars J, Bongers LJCM, van Laar-Van Schuppen S, Plant J, Mueller-Harvey I. Evaluating effects of tannins on extent and rate in vitro gas and methane production using an automated pressure evaluation system (APES). Anim Feed Sci Technol 2011b;166:377–90.

Pekkanen WF, Solarina S, Clark H. Reliability of the sulfur hexafluoride tracer technique for methane emission measurement from individual animals: an overview. Aust J Exp Agric 2008;48:223–9.

Pekkanen WF, Solarina S, Lassner M, Martin RJ, Molano G, Hernandez M, McLean S, Sondovale E, Luo D, Clark H. Assessment of the sulphur hexafluoride (SF6) tracer technique using respiration chambers for estimation of methane emissions from sheep. Anim Feed Sci Technol 2011;166–167:201–9.

Puchala R, Min BR, Goetsch AL, Sahlu T. Methane emissions by goats consuming Sericea lespedeza at different feeding frequencies. Anim Feed Sci Technol 2012a;175:76–84.
Puchala R, Ansimut G, Patra AK, Dewrelder GD, Wells JE, Varel VH, Sahlu T, Goetsch AL. Effects of different fresh-cut forages and their hays on feed intake, digestibility, heat production, and ruminal methane emissions by Boer x Spanish goats. J Anim Sci 2012;90:2754–62.

Reeve NJ, Nolling J, Morgan RM, Smith DR. Methanogenesis: genes, genomes, and who’s on first? J Bacteriol 1997;179:5975–86.

Rischewski J, Bielak A, Nürnberg G, Dermo M, Ruhla B. Ranking dairy cows for methane emissions measured using respiration chamber or GreenFeed tech- niques during early, peak, and late lactation. J Anim Sci 2017;95:3154–9.

Roehle R, Dewhurst RJ, Duthie CA, Rooke JA, McKain N, Ross DW, Hyslop JJ, Waterhouse A, Freeman TC, Watson M, Wallace RJ. Bovine host genetic variation influences rumen microbial methane production with best selection criterion for low methane emitting and efficiency feeding converting hosts based on methanogenic gene abundance. Front in Vet Sci 2016;3:1–20.

Rojas-Dowong RC, Zhong Y, Saffron CM, Liao W. Life cycle and economic assessment of anaerobic co-digestion of dairy manure and food waste. Ind Biotechnol 2015;11:127–39.

Ross EM, Moate PJ, Maretz L, Cocks BG, Hayes BJ. The effect of methane mitigation diets on the rumen microbiome using massively parallel sequencing. J Dairy Sci 2013;96:6030–46.

SAS. SAS institute user’s guide. Release 9.1.3. SAS Institute Inc.; 2004.

Shi W, Moon CD, Leahy SC, Kang D, Froula J, Kittelman J, et al. Methane yield phenotypes linked to differential gene expression in the sheep rumen micro- biome. Genome Res 2014;24:1517–25.

Silakunke N, Perevolotsky A, Provenza FD. Use of tannin-binding chemicals to assay for tannins and their negative postigestive effects in ruminants. Anim Feed Sci Technol 2001;91:69–81.

Slivinski BJ, Kreuzer M, Sutter FA, Machmuller HR. Body composition, milk protein content and body fat content from dairy cows fed diets supplemented with different plant extracts. J Anim Feed Sci 2004;13:73–91.

Strom G. Effect of botanically diverse pastures on the milk fatty acid profile. Master thesis. Department of Animal Nutrition and Man- agement, Swedish University of Agricultural Sciences; 2012.

Tajima K, Aminov R, Nagamine T, Matsu i H, Nakamura M, Benno Y. Diet-dependent shifts in the bacterial population of the rumen revealed with real-time PCR. Appl Environ Microbiol 2001;67:2766–74.

Tavendale MH, Moagher LP, Pacheco D, Walker N, Atwood GT, Sivakumar S. Methane production from in vitro rumen incubations with Lotus pedunculatus and Medicago sativa, and effects of extractable condensed tannin fractions on methanogenesis. Anim Feed Sci Technol 2005;123–124:403–19.

Tredschl LD, Fox DG, Guirao PJ, Baker MJ, Tylutki TP. Cornell value discovery system for individual cattle management. Dept. of Animal Science 2001:130.

Thompson DJ, Beever DE, Haines MJ, Cammell SB, Evans RT, Dhanoa MS, Austin AR. The yield and composition of the milk from Fresian cows grazing either perennial ryegrass or white clover in early lactation. J Dairy Res 1985;52:17–31.

Tiernan TT, Lascano CE, Kreuzer M, Hess HD. The ruminal degradability of fibre explains part of the low nutritional value and reduced methanogenesis in highly tanniferous tropical legumes. J Sci Food Agric 2008;88:1794–803.

Todd RW, Cole NA, Casey KD, Hagervoet R, Auermann BW. Methane emissions from southern high plains dairy wastewater lagoons in the summer. Anim Feed Sci Technol 2011;166:290–301.

Todd RW, Moffet C, Neel J, Turner K, Steiner J, Cole NA. Pasture-scale methane emissions of grazing cattle. Proc. Grazing CAP Field Res Sym 2016:46.

Tomkins NW, Denman SE, Pilajun R, Wanapat M, McSweeney CS, Elliott R. Rice straw and melon straw as feedstuffs for low methane emitting and efficient feeding systems. Anim Feed Sci Technol 2011;166:255–71.

Woodford SL, Waghorn GC, Hegarty RS. Lowering ruminant methane emissions through improved feed conversion efficiency. Anim Feed Sci Technol 2011;160:290–301.

Woolford SL, Waghorn GC, Laboyrie PG. Condensed tannins in birdsfoot trefoil (Lotus corniculatus) reduce methane emissions from dairy cows. Proc N Z Soc Anim Prod 2002;62:227–30.

Woolford SL, Waghorn GC, Laboyrie PG. Condensed tannins in birdsfoot trefoil (Lotus corniculatus) reduce methane emissions from dairy cows. Proc N Z Soc Anim Prod 2004;64:160.

Zimmerman PR. System for measuring metabolic gas emissions from animals. J Bacteriol 1997;179:5975–83.

Zimmerman, assignee; 2012. U.S. Patent 5,265,618.

University Corp for Atmospheric Research (UCAR); 1993. Assignee Pat No: 5,265,618.

Zhou M, Hernandez-Sanabria E, Guan LL. Characterization of variation in rumen microbial community structure in New Zealand dairy cows. Master thesis. Department of Animal Nutrition and Man- agement, Swedish University of Agricultural Sciences; 2012.

Zimmerman PR. System for measuring metabolic gas emissions from animals. University Corp for Atmospheric Research (UCAR); 1993. Assignee Pat No: 5,265,618.

Zimmerman PR. Methane mitigation strategies for livestock: Fundamentals and promises. Animal Nutrition 6 (2020) 231–246.