



Are dietary strategies to mitigate enteric methane emission equally effective across dairy cattle, beef cattle, and sheep?

Sanne van Gastelen,^{1,2*} Jan Dijkstra,¹ and André Bannink²

¹Animal Nutrition Group, Wageningen University & Research, PO Box 338, 6700 AH, Wageningen, the Netherlands

²Wageningen Livestock Research, Wageningen University & Research, PO Box 338, 6700 AH, Wageningen, the Netherlands

ABSTRACT

The digestive physiology of ruminants is sufficiently different (e.g., with respect to mean retention time of digesta, digestibility of the feed offered, digestion, and fermentation characteristics) that caution is needed before extrapolating results from one type of ruminant to another. The objectives of the present study were (1) to provide an overview of some essential differences in rumen physiology between dairy cattle, beef cattle, and sheep that are related to methane (CH₄) emission; and (2) to evaluate whether dietary strategies to mitigate CH₄ emission with various modes of action are equally effective in dairy cattle, beef cattle, and sheep. A literature search was performed using Web of Science and Scopus, and 94 studies were selected from the literature. Per study, the effect size of the dietary strategies was expressed as a proportion (%) of the control level of CH₄ emission, as this enabled a comparison across ruminant types. Evaluation of the literature indicated that the effectiveness of forage-related CH₄ mitigation strategies, including feeding more highly digestible grass (herbage or silage) or replacing different forage types with corn silage, differs across ruminant types. These strategies are most effective for dairy cattle, are effective for beef cattle to a certain extent, but seem to have minor or no effects in sheep. In general, the effectiveness of other dietary mitigation strategies, including increased concentrate feeding and feed additives (e.g., nitrate), appeared to be similar for dairy cattle, beef cattle, and sheep. We concluded that if the mode of action of a dietary CH₄ mitigation strategy is related to ruminant-specific factors, such as feed intake or rumen physiology, the effectiveness of the strategy differs across ruminant types, whereas if the mode of action is associated with methanogenesis-related fermentation pathways, the strategy is effective across ruminant types. Hence, caution is needed when translating ef-

fectiveness of dietary CH₄ mitigation strategies across different ruminant types or production systems.

Key words: methane, dietary strategy, ruminant, in vivo measurement

INTRODUCTION

Enteric fermentation enables ruminants to effectively turn human inedible biomass, such as coarse plant material, into high quality human-consumable protein in the form of milk and meat (Gerber et al., 2015), but this process also coincides with methane (CH₄) production by methanogenic *Archaea* (McAllister and Newbold, 2008). The amount of feed consumed and the composition of the diet have major impacts on enteric CH₄ production. Hence, several dietary strategies (e.g., supplementing lipids or specific additives, improving forage quality, feeding different forage types) to mitigate enteric CH₄ have been studied (e.g., Martin et al., 2010; Hristov et al., 2013a). Although all types of ruminant animals (e.g., cattle, goats, sheep) might have similar CH₄-forming pathways in the rumen, they differ considerably in their level of feed intake, rumen morphology, and rumen physiology. Consequently, the effectiveness of dietary strategies to mitigate CH₄ emission might also differ across different types of ruminants. The number of studies directly comparing rumen physiology across different types of ruminants is limited. Additionally, studies involving the evaluation of dietary CH₄ mitigation strategies in multiple ruminant types are lacking. Hence, in the present paper, we aimed (1) to provide a brief overview of differences in rumen physiology between dairy cattle, beef cattle, and sheep that are related to CH₄ emission; and (2) to evaluate whether dietary strategies to mitigate CH₄ emission with various modes of action are equally effective in dairy cattle, beef cattle, and sheep.

MATERIALS AND METHODS

To evaluate whether CH₄-mitigating dietary strategies with various modes of action are equally effective in dairy cattle, beef cattle, and sheep, we first identi-

Received October 2, 2018.

Accepted March 12, 2019.

*Corresponding author: sanne.vangastelen@wur.nl

fied key areas of differences directly related to rumen physiology and rumen functioning, including feed intake level, ruminal degradation, passage rate and mean retention time (**MRT**), rumen fermentation parameters, rumen microbial community, total-tract digestibility, and ruminant genotype.

Second, we performed a literature search to evaluate the effectiveness of CH₄ mitigation strategies, using Web of Science (Thomson Reuters Science, New York, NY) and Scopus (Elsevier, Amsterdam, the Netherlands), with a focus on forage quality, forage type and forage replacement, forage to concentrate ratio, and feed additives that have been tested in multiple ruminant types. These dietary strategies are recommended CH₄-mitigation practices according to a review by Hristov et al. (2013a,b). Scientific papers were selected if they met all the following criteria: (1) an in vivo experiment was conducted; (2) the CH₄ emissions were measured directly (i.e., not estimated); (3) the composition of the basal diet was described; (4) the results were available on DMI, and on CH₄ production (g/d) or CH₄ yield [g/kg of DMI or % of gross energy intake (**GEI**)]; and (5) a statistical analysis was performed. Although preferred, the studies did not have to involve the testing of dietary strategies in multiple types of ruminants. A total of 94 studies were selected.

The effect size of the dietary strategies was determined for each individual study, expressed as a proportion (%) of the CH₄ emission for the control treatment and based on the reported treatment means [percentage increase or decrease relative to the value established with the “baseline” or control treatment (e.g., the percentage change in CH₄ emission with supplementation of the highest nitrate dose compared with no supplementation of nitrate)]. The level of DMI and CH₄ emission varies greatly across studies and from one type of ruminant to another. Hence, comparing the size of the effect in absolute terms (e.g., kg/d for DMI and g/d or g/kg of DMI for CH₄) is difficult. Expressing effect size as a percentage therefore served as a more feasible alternative. The size of effect was calculated including all studies, irrespective of whether significant differences were reported by the respected studies. If fewer than 3 studies per dietary strategy × ruminant type were available, however, the studies were only included in the tables to provide a complete overview but not used to calculate effect sizes or used to formulate conclusions.

RESULTS AND DISCUSSION

Comparative Rumen Physiology

The total daily CH₄ production of a sheep is typically only 12% of that of a dairy cow (Ulyatt et al., 2002).

However, results are less consistently reported for CH₄ expressed per unit of feed intake [g/kg of DMI or as a percent of GEI; e.g., Blaxter and Wainman, 1961; Swainson et al., 2008]. Although studies comparing rumen digestive physiology across different ruminant types are limited, some have argued that differences in fractional passage rate, rumen fermentation conditions, and apparent digestibility across ruminant types caused differences in CH₄ yield (both as g/kg of DMI and as % of GEI; Aerts et al., 1984; Pearson et al., 2006), whereas others have argued that differences in microbial populations and site of digestion were responsible for differences in CH₄ yield across ruminant types (e.g., Swainson et al., 2008).

Feed Intake Level

On a daily basis, in grams per day, it is obvious that both dairy and beef cattle have a higher DMI capacity and a higher realized DMI than sheep because of their larger body size, greater nutritional requirements, and larger rumen capacity. Soto-Navarro et al. (2014) demonstrated that beef cattle consumed more feed than sheep when DMI was expressed per unit of metabolic BW. However, as forage quality decreased (lower OM digestibility, **OMD**), this difference in DMI relative to metabolic BW became smaller. Colucci et al. (1989) observed a depression in digestibility of different feed fractions with increasing feed intake for dairy cattle and sheep. This is most likely the result of a shorter MRT in the rumen, increased fractional passage rate, and decreased ruminal fermentation for both dairy cattle and sheep as feed intake increases. Notably, the depression of digestibility appeared to be greater for cattle than for sheep, most likely because cattle appear to have a lower digestive capacity than sheep (Colucci et al., 1989).

Ruminal Degradation

Siddons and Paradine (1983) demonstrated that in situ rumen degradation of several feedstuffs was lower for beef steers than for sheep, irrespective of incubation time. Lower fractional degradation rates in beef and dairy cattle than in sheep have been observed in other studies as well (e.g., Poppi et al., 1981; Udén and Van Soest, 1984; Šebek and Everts, 1999). These observed differences between cattle and sheep in in situ fractional degradation rates may have several causes, such as differences in the rations offered, differences in in situ techniques, and differences in the amount of nutrient recycling in the rumen (Lindberg, 1985; Nocek, 1988). The consistent findings reported across the literature indicate that differences in rumen fractional degrada-

tion kinetics between cattle (beef and dairy) and sheep are not caused by methodological differences alone, but are also due to between-ruminant differences. It has been suggested that differences in feed fractional degradation rates in the rumen might be caused by lower rumen ammonia levels in dairy and beef cattle compared with sheep (Poppi et al., 1981; Siddons and Paradine, 1983). Other factors that may play a role are body size and, subsequently, rumen size and rumen fluid volumes (Lechner-Doll et al., 1991), as well as feed intake relative to rumen volume, passage rate, and ruminal pH.

Passage Rate and MRT

The passage rate of digesta through the digestive tract, particularly through the rumen, has been linked to CH₄ emissions (Swainson et al., 2008). Okine et al. (1989) reported significant inverse relationships between fractional passage rate constants of both ruminal fluid and particulate matter and CH₄ production in beef steers. Low CH₄ yield (g/kg of DMI) of sheep was associated with shorter MRT of liquid and of particulate digesta (Goopy et al., 2014). The association between CH₄ emissions and both fractional passage rate and MRT seems to apply to beef cattle and sheep, and most likely to dairy cattle as well. Therefore, it is important to know whether there are differences across ruminant types in terms of fractional passage rate or MRT, as this may affect the CH₄ mitigation potential of a dietary strategy.

Lechner-Doll et al. (1991) compared retention times of fluid and small particles in the rumen of zebu cattle and 2 breeds of indigenous sheep. The MRT of fluid in the rumen was similar for both ruminant types (approximately 10 h), whereas the labeled particles were retained substantially longer for cattle (28 h) than for sheep (20 h). This was consistent with the findings of Reid et al. (1990), Prigge et al. (1984), and Colucci et al. (1990). These results imply that particles are more selectively retained in the rumen of cattle compared with sheep, and that this selective retention is not affected by variation in MRT arising from changes in feed intake level or feed quality (e.g., Grovum and Williams, 1977; Lindberg, 1988).

Rumen Fermentation Parameters

Rumen fermentation characteristics may or may not differ between different types of ruminants, depending on the type of diet fed and the amount of feed consumed relative to rumen volume. When sheep and beef steers were fed similar diets at maintenance level, Siddons and Paradine (1983) reported a higher total

VFA concentration and molar proportion of propionate in beef steers than in sheep, whereas the molar proportion of acetate was lower. However, Norton et al. (1994) reported a higher molar proportion of butyric acid and lower proportion of acetic acid in beef steers than in sheep for both a molasses diet and a sorghum grain diet, but a lower proportion of propionic acid in beef steers than in sheep was observed only on a molasses diet and not on a sorghum grain diet. Soto-Navarro et al. (2014) demonstrated that ruminal pH was influenced by a ruminant × forage quality interaction. Ruminal pH was higher for sheep than for beef steers when alfalfa hay was fed but did not differ when grass hay or lovegrass hay was fed.

Rumen Microbial Community

Henderson et al. (2015) determined the effect of multiple factors on rumen microbial community composition across a wide geographical range. The differences in composition of microbial communities were predominantly attributed to diet, but an effect of host was also found. Microbial communities could clearly be discriminated by host (i.e., bovines, including dairy and beef cattle, vs. caprids, including sheep), with bacteria, rather than *Archaea* or protozoa, being the main drivers behind the observed differences. Further, Jeyanathan et al. (2011) reported similar archaeal communities in the rumen of nonlactating dairy cattle and sheep, suggesting a common core of ruminal methanogen species in ruminants. This suggests that the main players in the CH₄ production pathway are similar across ruminant types, indicating a similar effectiveness if a dietary strategy targeted the methanogens directly.

Total-Tract Digestibility

Hindgut fermentation contributes to digestion in the total gastrointestinal tract of ruminants. However, enteric fermentation, and consequently CH₄ production, occurs predominantly within the rumen (~87%) and to a small extent in the large intestines (~13%; Murray et al., 1976). In addition, CH₄ production per unit of fermented nutrients in the hindgut is generally lower compared with CH₄ production per unit of fermented nutrients in the rumen. This is mainly because hindgut fermentation differs from ruminal fermentation (due to absence of active protozoa; Fievez et al., 1999). Therefore, discussion in this section has been limited specifically to digestion within the rumen. Greater digestibility values for OM and fiber have been reported for dairy and beef cattle than for sheep (e.g., Blaxter et al., 1966; Leaver et al., 1969; McDonald et al., 2002; Pearson et al., 2006) and the difference in digestive

Table 1. The effect of increased digestibility on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurement	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Grass herbage and silage								
Gordon et al., 1995	Dairy cattle	Respiratory chamber (RC)	±50:50 ⁴	Perennial ryegrass silage, ad libitum; from late harvest to early harvest primary growth	=	=	ND ⁵	ND
Brask et al., 2013	Dairy cattle	RC	65:35	Perennial ryegrass-clover silage, ad libitum; from late harvest to early harvest primary growth	+	=	-	ND
Warner et al., 2015	Dairy cattle	RC	85:15	Perennial ryegrass herbage, restricted; from 5 to 3 wk regrowth after initial cut	=	=	=	-
Warner et al., 2016	Dairy cattle	RC	80:20	Perennial ryegrass silage, restricted; from 62 to 41 to 28 d of regrowth	+	+	-	-
Warner et al., 2017	Dairy cattle	RC	80:20	Perennial ryegrass silage, 15.5 kg of DM/d; from late heading to early heading to boot to leafy	+	-	-	-
Warner et al., 2017	Dairy cattle	RC	80:20	Perennial ryegrass silage, 16.6 kg of DM/d; from late heading to early heading to boot to leafy	+	-	-	-
Dini et al., 2017	Dairy cattle ⁶	SF ₆ -tracer technique (SF ₆)	100:0	Pastures with 2 divergent qualities, ad libitum; on average 44 vs. 60% OM digestibility (OMD)	+	+	-	-
Boadi and Wittenberg, 2002 ⁷	Dairy cattle	SF ₆	100:0	Grass hay, ad libitum; from 38.5 to 50.7 to 61.5% in vitro OMD (IVOMD)	+	+	=	ND
Boadi and Wittenberg, 2002 ⁷	Dairy cattle	SF ₆	100:0	Grass hay, restricted; from 38.5 to 50.7 to 61.5% IVOMD	+	=	=	ND
Boadi and Wittenberg, 2002 ⁷	Beef cattle	SF ₆	100:0	Grass hay, ad libitum; from 38.5 to 50.7 to 61.5% IVOMD	+	+	=	ND
Boadi and Wittenberg, 2002 ⁷	Beef cattle	SF ₆	100:0	Grass hay, restricted; from 38.5 to 50.7 to 61.5% IVOMD	+	=	=	ND
Pinares-Patino et al., 2003	Beef cattle	SF ₆	100:0	Timothy pasture, ad libitum; from senescence to flowering to heading to early vegetative	=	=	ND	ND
Hart et al., 2009	Beef cattle	SF ₆	100:0	Perennial ryegrass herbage, ad libitum; from low to high DM digestibility	+	+	=	ND
Jonker et al., 2016a, experiment 1	Beef cattle	RC	100:0	Perennial ryegrass herbage, 1.5 × ME; from mature to vegetative	=	+	=	ND
Jonker et al., 2016a, experiment 2	Beef cattle	RC	100:0	Perennial ryegrass herbage, 1.8 × ME; from mature to vegetative	-	-	=	ND
Jonker et al., 2016a, experiment 3	Beef cattle	RC	100:0	Perennial ryegrass herbage, 1.1 × ME; from mature to vegetative	-	-	+	ND
Armstrong, 1964	Sheep	RC	100:0	Ryegrass S23, 1.0 × ME and ad libitum; from seed setting to head emergence to late leafy to young leafy	=	ND	ND	ND
Armstrong, 1964	Sheep	RC	100:0	Ryegrass S24, 1.0 × ME and ad libitum; from 20% heads emerged to late leafy	=	ND	ND	ND
Armstrong, 1964	Sheep	RC	100:0	Timothy S48, 1.0 × ME and ad libitum; from 100% heads emerged to 60% heads emerged to late leafy	=	ND	ND	ND
Armstrong, 1964	Sheep	RC	100:0	Cocksfoot S37, 1.0 × ME and ad libitum; from 100% heads emerged to 60% heads emerged to late leafy	=	ND	ND	ND
Molano and Clark, 2008	Sheep	SF ₆	100:0	Perennial ryegrass herbage, 0.75 to 2.00 × ME; from reproductive to vegetative phase	=	=	=	ND
Amaral et al., 2016	Sheep	SF ₆	100:0	Pearl millet swards with different N fertilization doses, ad libitum; 50 vs. 100 vs. 200 vs. 400 kg of N/ha	=	-	=	ND

Continued

Table 1 (Continued). The effect of increased digestibility on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurement	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Other forages								
Cammell et al., 2000	Dairy cattle	RC	±56:44 ⁸	Corn silage, ad libitum; 380 vs. 330 vs. 280 vs. 230 g of DM/kg of fresh weight	=	ND	=	ND
Hatew et al., 2016	Dairy cattle	RC	80:20	Corn silage, restricted; 40 vs. 32 vs. 25% of DM	=	+ ⁹	+ ¹⁰	+ ⁹
Mc Geough et al., 2010a	Beef cattle	SF ₆	±77:23 ¹¹	Corn silage, ad libitum; 33.3 vs. 33.9 vs. 31.5 vs. 27.7% of DM	= ¹⁰	=	+ ⁹	+ ⁹

¹Where +, -, and = refer to increase ($P < 0.10$), decrease ($P < 0.10$), and no difference ($P > 0.10$), respectively, between the 2 most extreme dietary treatments.

²Forage to concentrate ratio.

³Methane production in g, L or MJ per day; methane yield in g, L or MJ per kg of DMI; methane energy as % of gross energy intake; methane intensity in g, L or MJ per kg product (e.g., milk yield and BW gain).

⁴Forage was fed ad libitum, always supplemented with 10.0 kg of concentrate/d. This resulted in forage content in diet ranging from 50 to 54%.

⁵Not determined.

⁶Nonlactating heifers.

⁷High-quality diet (61.5% IVOMD) consisted of a mixture of legume and grass hay, whereas both medium-quality (50.7%) and low-quality (38.5%) diets consisted of only grass hay.

⁸Forage was fed ad libitum, always supplemented with 8.7 kg of concentrate DM/d. This resulted in the forage content in the diet ranging from 55 to 57%.

⁹Linear effect.

¹⁰Quadratic effect.

¹¹Forage was fed ad libitum, always supplemented with 2.57 kg of concentrate DM/d. This resulted in the forage content in the diet ranging from 76 to 79%.

capacity appears to become larger as roughage quality decreases (Rees and Little, 1980; Aerts et al., 1984; Prigge et al., 1984; Soto-Navarro et al., 2014). This suggests that when fed a low-quality roughage, dairy and beef cattle appear to have a greater capacity to digest nutrients, in particular fiber and OM compared with sheep. According to Poppi et al. (1980) and Aerts et al. (1984), this may result from ruminal MRT. Sheep, on the other hand, appear to have a greater capacity to digest proteins. Alexander et al. (1962), Aerts et al. (1984), and Südekum et al. (1995) reported that sheep had a greater ability to digest CP than dairy and beef cattle, especially when low-protein forages were fed.

Ruminant Genotype

Overall, literature findings indicate that the digestive physiology of ruminants is sufficiently different to recommend caution in the extrapolation of the perceived efficacy of CH₄-mitigating dietary strategies from one ruminant type to another. It should be noted that a significant proportion of the literature findings in the current overview were reported two or more decades ago. Developments in management and breeding of ruminant animals in the past decades may have affected elements of digestive physiology and the differences across ruminant types. Potts et al. (2017) reported a decline in feed digestibility in dairy cattle between 1970 and 2014, mainly caused by an increased passage rate of feed through the digestive tract. No such developments in intake and digestibility in time are known for sheep, although we expect that such developments have been far more pronounced in cattle than in sheep. We therefore suggest that the observed differences between dairy cattle, beef cattle, and sheep in studies from the 1980s or earlier might not be presently valid due to the development of ruminants and ruminant production systems since that time (e.g., breeding and management factors). Unfortunately, comparative studies from recent years are lacking, and confirming these previous findings proves challenging. That being said, it is important to note that studies describing dietary CH₄ mitigation strategies are predominantly from the last 2 decades. Hence, caution should be taken when using results from comparative physiology studies conducted before 1980s to explain differences observed across ruminant types in the effectiveness of dietary CH₄ mitigation strategies.

Comparative Effects of Dietary Strategies on Methanogenesis

Tables 1 to 6 summarize the studies used to determine the effect of several CH₄-mitigating dietary strate-

Table 2. The effect of replacing different forage types (e.g., grass silage and alfalfa silage) with corn silage on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Waldo et al., 1997	Dairy cattle ⁴	Respiratory chamber (RC)	89:11 ⁵	Replacing alfalfa silage with corn silage combined with a protein-rich concentrate, low (725 g/d) and high (950 g/d) daily gain; 0 vs. 100% replacement	+	ND ⁶	ND	ND
Waugh et al., 2005	Dairy cattle	SF ₆ -tracer technique (SF ₆)	100:0	Replacing perennial ryegrass pasture with corn silage, ad libitum; 0 vs. 12 vs. 24 vs. 36% replacement	=	+	+	+
Hindrichsen et al., 2006	Dairy cattle	RC	100:0	Replacing hay and grass silage-based forage with grass silage and corn silage-based forage, restricted; 0 vs. 100% replacement	=	=	=	=
Hindrichsen et al., 2006	Dairy cattle	RC	50:50	Replacing hay and grass silage-based forage with grass silage and corn silage-based forage, restricted; 0 vs. 100% replacement	=	=	=	=
McCourt et al., 2007	Dairy cattle	RC	75:25 ⁷	Replacing grass silage with corn silage, ad libitum; 0 vs. 100% replacement	+	+	=	ND
McCourt et al., 2007	Dairy cattle	RC	75:25 ⁷	Replacing whole crop wheat with corn silage, ad libitum; 0 vs. 100% replacement	=	=	=	ND
Reynolds et al., 2010	Dairy cattle	RC	50:50	Replacing grass silage with corn silage, ad libitum; 75:25 vs. 25:75 grass silage to maize silage ratio	+	=	=	ND
Brask et al., 2013	Dairy cattle	RC	65:35	Replacing grass-clover silage with corn silage, ad libitum; 0 vs. 100% replacement	=	=	=	ND
Hassanat et al., 2013	Dairy cattle	RC	60:40	Replacing alfalfa silage with corn silage, ad libitum; 0 vs. 50 vs. 100% replacement	+	+	+	+
Benchaaar et al., 2014	Dairy cattle	RC	60:40	Replacing barley silage with corn silage, ad libitum; 0 vs. 50 vs. 100% replacement	+	+	+	+
Doreau et al., 2014	Dairy cattle	SF ₆	45:55	Replacing grass silage with corn silage, restricted; 0 vs. 100% replacement	=	=	=	=
Arndt et al., 2015	Dairy cattle	RC	55:45	Replacing alfalfa silage with corn silage, ad libitum; 20 vs. 40 vs. 60 vs. 80% replacement	=	=	=	=
Van Gastellen et al., 2015	Dairy cattle	RC	80:20	Replacing grass silage with corn silage, restricted; 0 vs. 33 vs. 67 vs. 100% replacement	+	+	+	+
Günal et al., 2018	Dairy cattle	RC	74:26 ¹⁰	Replacing grass silage with corn silage, ad libitum; 0 vs. 100% replacement	+	+	=	ND
Günal et al., 2018	Dairy cattle	RC	78:22 ¹¹	Replacing grass silage with whole-crop wheat silage, ad libitum; 0 vs. 100% replacement	+	=	=	ND
Mc Geough et al., 2010b ¹²	Beef cattle	SF ₆	73:27 ¹³	Replacing grass silage with wheat silage, ad libitum; 0 vs. 100% replacement	+	=	=	=
Doreau et al., 2011	Beef cattle	SF ₆	50:50 ¹⁴	Replacing natural grassland hay with corn silage, ad libitum; 0 vs. 100% replacement	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 5 mo	RC	57:43 ¹⁵	Replacing grass silage with corn silage, ad libitum; 0 vs. 100% replacement	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 9 mo	RC	74:26 ¹⁶	Replacing grass silage with corn silage, ad libitum; 0 vs. 100% replacement	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 11 mo	RC	73:27 ¹⁷	Replacing grass silage with corn silage, ad libitum; 0 vs. 100% replacement	=	=	+	ND
Jonker et al., 2016a, experiment 3	Beef cattle	RC	100:0	Replacing vegetative perennial ryegrass pasture with corn silage, 1.1 × ME; 0 vs. 100% replacement	=	=	=	ND
Jonker et al., 2016a, experiment 3	Beef cattle	RC	100:0	Replacing mature perennial ryegrass pasture with corn silage, 1.1 × ME; 0 vs. 100% replacement	=	=	=	ND

Continued

Table 2 (Continued). The effect of replacing different forage types (e.g., grass silage and alfalfa silage) with corn silage on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Jonker et al., 2016a, experiment 4	Beef cattle	RC	100:0	Replacing perennial ryegrass pasture with corn silage, 1.6 × ME; 0 vs. 35% replacement	=	=	+	ND
Margan et al., 1994	Sheep	RC	100:0	Replacing dried red clover with corn silage, ad libitum; 1:0 vs. 2:1 vs. 1:2 vs. 0:1 red clover to corn silage ratio	- ⁸	=	ND	ND
Margan et al., 1994	Sheep	RC	100:0	Replacing dried red clover with corn silage, restricted; 1:0 vs. 2:1 vs. 1:2 vs. 0:1 red clover to corn silage ratio	=	=	ND	ND
Jonker et al., 2016b	Sheep	RC	100:0	Replacing alfalfa silage with corn silage, 2% of BW; 0 vs. 25 vs. 50 vs. 75% vs. 100% replacement ¹⁸	=	= ⁸	= ⁸	= ⁸ ND

¹Where +, -, and = refer to increase ($P < 0.10$), decrease ($P < 0.10$) and no difference ($P > 0.10$), respectively, between the 2 most extreme dietary treatments.

²Forage to concentrate ratio.

³Methane production in g, L or MJ per day; methane yield in g, L or MJ per kg of DMI; methane energy as % of gross energy intake; methane intensity in g, L or MJ per kg product (e.g., milk yield and BW gain).

⁴Nonlactating Holstein heifers.

⁵Different F:C ratios; the alfalfa silage based-diet (with a 100:0 F:C ratio) was replaced by a corn silage-based diet combined with a protein-rich concentrate (with a 78:22 F:C ratio).

⁶Not determined.

⁷Forage was fed ad libitum, always supplemented with 5 kg of concentrate/d. This resulted in the forage content in the diet ranging from 70 to 77%.

⁸Quadratic effect.

⁹Linear effect.

¹⁰Forage was fed ad libitum, always supplemented with 5.5 kg of concentrate/d. This resulted in the forage content in the diet ranging from 70 to 77%.

¹¹Forage was fed ad libitum, always supplemented with 5.5 kg of concentrate/d. This resulted in the forage content in the diet ranging from 77 to 79%.

¹²This study involved wheat silage rather than corn silage.

¹³The dietary treatments had a different F:C ratio, with the forage content ranging from 53 to 89%.

¹⁴Different F:C ratios; hay based diet consisted of 49% natural grassland hay, 41% ground corn grain, and 10% soybean meal, whereas the corn silage based diet consisted of 63% corn silage, 21% ground corn grain, and 16% soybean meal.

¹⁵Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 56 to 60%.

¹⁶Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 72 to 77%.

¹⁷Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 70 to 75%.

¹⁸The 100% alfalfa silage replacement diet contained 92% corn silage and 8% soybean meal.

Table 3. The effect of replacing grass silage with legumes or tannin-rich forages on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Legumes								
Lee et al., 2004	Dairy cattle	SF ₆ -tracer technique (SF ₆)	100:0	Replacing perennial ryegrass with white clover, ad libitum; 0 vs. 15 vs. 30 vs. 60% replacement	+	-	-	=
Van Dorland et al., 2007, experiment 2	Dairy cattle	Respiratory chamber (RC)	100:0 ⁴	1,000 g/kg perennial ryegrass replaced with 411 g/kg white-clover and 589 g/kg perennial ryegrass silage, ad libitum	=	+	ND ⁵	=
Van Dorland et al., 2007, experiment 2	Dairy cattle	RC	100:0	1,000 g/kg perennial ryegrass replaced with 391 g/kg red-clover and 609 g/kg perennial ryegrass silage, ad libitum	=	=	ND	=
Enriquez-Hidalgo et al., 2014	Dairy cattle	SF ₆	93:7 ⁶	Replacing grass-only swards with grass and white clover swards (containing 20% white clover), ad libitum; 0 vs. 100% replacement	+	=	-	=
McCaughy et al., 1999	Beef cattle	SF ₆	100:0	Replacing grass-only pasture with alfalfa-grass pasture (containing 78% alfalfa and 22% grass), ad libitum; 0 vs. 100% replacement	+	+	ND	ND
Carulla et al., 2005	Sheep	RC	100:0	Replacing perennial ryegrass with red clover, ad libitum; 1:0 vs. 1:1	=	=	+	ND
Carulla et al., 2005	Sheep	RC	100:0	Replacing perennial ryegrass with alfalfa, ad libitum; 1:0 vs. 1:1	=	=	=	ND
Hammond et al., 2013, experiment 1	Sheep	RC	100:0	Replacing perennial ryegrass to alfalfa ratio	-	-	-	ND
Hammond et al., 2013, experiment 2	Sheep	RC	100:0	Replacing perennial ryegrass pasture with fresh white clover pasture, 1.6 × ME; 0 vs. 100% replacement	=	=	=	ND
Hammond et al., 2013, experiment 3	Sheep	RC	100:0	Replacing perennial ryegrass pasture with fresh white clover pasture, 0.8 × ME; 0 vs. 100% replacement	=	=	=	ND
Woodward et al., 2001	Sheep	RC	100:0	Replacing perennial ryegrass pasture with fresh white clover pasture, 2.0 × ME; 0 vs. 100% replacement	=	=	+	ND
Woodward et al., 2004	Sheep	RC	100:0	Replacing perennial ryegrass pasture with fresh white clover pasture, 1.6 × ME; 0 vs. 100% replacement	-	=	=	ND
Huyen et al., 2016	Dairy cattle	SF ₆	100:0	Replacing perennial ryegrass silage with birdsfoot trefoil (<i>Lotus corniculatus</i>) silage, ad libitum; 0 vs. 100% replacement	+	=	-	ND
De Oliveira et al., 2007	Beef cattle	SF ₆	40:60	Replacing a low-tannin sorghum silage (0.2 g/kg of DM; BR700), 1.0 × ME; 0 vs. 100% replacement	=	=	=	ND
De Oliveira et al., 2007	Beef cattle	SF ₆	100:0	Replacing a low-tannin sorghum silage (0.2 g/kg of DM; IF305) with a high-tannin sorghum silage (1.0 g/kg of DM; BR 700), 1.0 × ME; 0 vs. 100% replacement	=	=	=	ND
Tiemann et al., 2008	Sheep	RC	100:0	550 g/kg brachiaria + 450 g/kg vicia legume; replacing vicia legume with <i>Calliandra calothyrsus</i> , 60 g/kg of BW ^{0.75} ; 0 vs. 33 vs. 67% replacement	- ⁷	- ⁸	- ⁷	ND
Tiemann et al., 2008	Sheep	RC	100:0	550 g/kg brachiaria + 450 g/kg vicia legume; replacing vicia legume with <i>Flemingia macrophylla</i> , 60 g/kg of BW ^{0.75} ; 0 vs. 33 vs. 67% replacement	=	- ⁷	- ⁷	ND
Delgado et al., 2013	Sheep	RC	Variable ⁹	Replacing concentrate with <i>Leucaena leucocephala</i> , ad libitum; 0 vs. 27% replacement	=	=	-	ND

Continued

Table 3 (Continued). The effect of replacing grass silage with legumes or tannin-rich forages on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	CH ₄ emissions ³				
					DMI (kg/d)	Production	Yield	Energy	Intensity
Archimède et al., 2016	Sheep	SF ₆	100:0 ¹⁰	Replacing tropical natural grassland supplemented with <i>Glyricidia sepium</i> [39 g of condensed tannins (CT)/kg of DM] pellets, ad libitum; 0 vs. 44% replacement	+	=	-	ND	ND
Archimède et al., 2016	Sheep	SF ₆	100:0 ¹⁰	Replacing tropical natural grassland supplemented with <i>Leucaena leucocephala</i> (75 g of CT/kg of DM) pellets, ad libitum; 0 vs. 44% replacement	+	=	-	ND	ND
Archimède et al., 2016	Sheep	SF ₆	100:0 ¹⁰	Replacing tropical natural grassland supplemented with <i>Manihot esculenta</i> (92 g of CT/kg of DM) pellets, ad libitum; 0 vs. 44% replacement	+	=	-	ND	ND

¹Where +, -, and = refer to increase ($P < 0.10$), decrease ($P < 0.10$) and no difference ($P > 0.10$), respectively, between the 2 most extreme dietary treatments.

²Forage to concentrate ratio.

³Methane production in g, L or MJ per day; methane yield in g, L or MJ per kg of DMI; methane energy as % of gross energy intake; methane intensity in g, L or MJ per kg product (e.g., milk yield and BW gain).

⁴A maximum of 2 kg/d hay was offered and pelleted barley was fed in amounts to meet energy requirements for milk production.

⁵Not determined.

⁶Cows received 1 kg of concentrates per day, which equals a F:C ratio of 93:7 for the ryegrass swards and a F:C ratio of 94:6 for the grass and white clover swards.

⁷Linear effect.

⁸Quadratic effect.

⁹Different F:C ratios: control diet consisted of 63% *Pennisetum purpureum* (clone CT-169) and 37% concentrate, whereas the experimental diets consisted of 63% *P. purpureum*, 27% *Leucaena leucocephala*, and 10% concentrate.

¹⁰The tannin-rich forages tested were given in pellet form.

gies on the response variables DMI and CH₄ emission expressed in multiple units (i.e., production: L/d per animal or g/d per animal; yield: L/kg of DMI, g/kg of DMI, or % of GEI; intensity: g/kg of product, with product being milk yield for dairy cattle and ADG for beef cattle and sheep). The symbols used in the tables (i.e., -, +, and =) illustrate whether the response variables were affected; that is, decreased ($P \leq 0.10$), increased ($P \leq 0.10$), or unaffected ($P > 0.10$), respectively. If more than 2 dietary treatments were applied in a study, the effect on the response variables was rated for the extremes of the treatments of interest (e.g., a diet of lowest digestibility vs. a diet of highest digestibility). If reported, we indicated whether a linear or quadratic effect was found in the respective studies.

Forage Quality

Table 1 summarizes the studies that investigated the effect of forage digestibility (grass herbage, grass silage, and corn silage) on CH₄ emission from dairy cattle, beef cattle, and sheep. Improved digestibility, as reflected by OMD, of grass herbage or grass silage (on average 25%) for dairy cattle increased DMI (on average 14%) and CH₄ production (g/d; on average 8%), whereas CH₄ yield (g/kg of DMI or as % of GEI) and, if available, CH₄ intensity (g/kg of milk) decreased 10 and 19%, respectively, on average. For beef cattle, DMI and CH₄ production also increased (on average, 10 and 7%, respectively), but CH₄ yield (both in g/kg of DMI and as % of GEI) was unaffected with improved OMD (average 33% OMD improvement). For sheep, improved OMD (on average 17%) did not affect DMI but increased CH₄ yield (% of GEI) 7%. The number of studies (3) on effect of increased digestibility of other forages was too small to allow quantitative evaluation. Upon an increase in digestibility of corn silage, CH₄ emissions were unchanged or increased for both dairy cattle and beef cattle; no data were available for sheep.

These results indicate that the effect of increased grass (herbage or silage) digestibility on CH₄ mitigation differs between ruminant types. This strategy seems to be the most effective for dairy cattle, whereas it is not effective for beef cattle, and has no or opposite effects in sheep. Feed allowance in all studies (dairy cattle, beef cattle, and sheep) ranged from restricted (based on free access feed intake for dairy cattle or on ME requirements for beef and sheep) to ad libitum. However, in all beef cattle and sheep studies, no concentrate was fed (F:C ratio of 100:0), whereas in 5 out of 7 dairy cattle studies, concentrate was fed. This difference in F:C ratio between studies on dairy cattle and those on beef cattle or sheep might explain part of the difference found across these ruminant types in

Table 4. The effect of increasing concentrate level on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ²		
					Production	Yield	Intensity
Tyrell and Moe, 1972	Dairy cattle	Respiratory chamber (RC)	Forage consisted of corn silage. Forage:concentrate (F:C) ratio, restricted: from 69:31 to 41:59 on DM basis	-	ND ³	-	ND
Ferris et al., 1999	Dairy cattle	RC	Forage consisted of grass silage. F:C ratio, ad libitum: 63:37 vs. 52:48 vs. 41:59 vs. 30:70 on DM basis	+	-	-	ND
Lovett et al., 2005	Dairy cattle	SF ₆ -tracer technique (SF ₆)	Herbage ⁴ voluntary intake with concentrate supplementation, ad libitum; 0.87 vs. 5.24 kg on DM basis	+	+	=	ND
Hindrichsen et al., 2006	Dairy cattle	RC	Forage consisted of grass silage and hay, 1.0 × NE _L . F:C ratio: 100:0 vs. 50:50 on DM basis	+	+	=	-
Hindrichsen et al., 2006	Dairy cattle	RC	Forage consisted of grass silage and corn silage, 1.0 × NE _L . F:C ratio: 100:0 vs. 50:50 on DM basis	+	=	-	=
Aguerre et al., 2011	Dairy cattle	RC	Forage consisted of alfalfa silage and corn silage in a 1:1 ratio, ad libitum. F:C ratio: 68:32 vs. 61:39 vs. 54:46 vs. 47:53 on DM basis	=	- ⁵	- ⁵	ND
Lovett et al., 2003	Beef cattle	SF ₆	Forage consisted of grass silage, ad libitum. F:C ratio: 65:35 vs. 40:60 vs. 10:90 on DM basis	+	+	- ⁶	- ⁶
Beauchemin and McGinn, 2005	Beef cattle	RC	Forage consisted of barley silage, concentrate contained steam-rolled barley, daily gain of 1.0 kg/d. F:C ratio: 70:30 vs. 9:91 on DM basis	=	-	-	ND
Beauchemin and McGinn, 2005	Beef cattle	RC	Forage consisted of corn silage, concentrate contained dry-rolled corn, daily gain of 1.0 kg/d. F:C ratio: 70:30 vs. 9:91 on DM basis	=	-	-	ND
De Oliveira et al., 2007	Beef cattle	SF ₆	Forage consisted of low-tannin sorghum (1F305), 1.0 × ME. F:C ratio: 100:0 vs. 40:60 on DM basis	+	+	=	ND
De Oliveira et al., 2007	Beef cattle	SF ₆	Forage consisted of high-tannin sorghum (BR700), 1.0 × ME. F:C ratio: 100:0 vs. 40:60 on DM basis	+	+	=	ND
Mc Geough et al., 2010b	Beef cattle	SF ₆	Forage consisted of whole crop wheat silage, ad libitum. F:C ratio: 89:11 vs. 79:21 vs. 69:31 vs. 53:47	+	- ⁶	- ⁵	- ⁵
Laegre et al., 2016	Beef cattle	SF ₆	Forage consisted of maize silage, ad libitum. F:C ratio: 60:40 vs. 40:60 on DM basis	=	=	=	ND
Moss et al., 1995	Sheep	RC	Forage consisted of grass silage, 1.0 × ME. F:C ratio: 100:0 vs. 76:24 vs. 51:49 vs. 26:74 on DM basis	- ^{5,7}	=	ND	+
Moss et al., 1995	Sheep	RC	Forage consisted of grass silage, 1.5 × ME. F:C ratio: 100:0 vs. 78:22 vs. 54:46 vs. 28:72 on DM basis	- ^{5,7}	- ⁶	ND	ND
Liu et al., 2012, fall	Sheep	SF ₆	Forage consisted of cornstalk silage, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	+	=	=	ND
Liu et al., 2012, fall	Sheep	SF ₆	Forage consisted of dry cornstalk, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	+	=	-	ND
Liu et al., 2012, winter	Sheep	SF ₆	Forage consisted of cornstalk silage, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	=	=	=	ND
Liu et al., 2012, winter	Sheep	SF ₆	Forage consisted of dry cornstalk, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	+	-	-	ND
Liu et al., 2012, spring	Sheep	SF ₆	Forage consisted of cornstalk silage, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	+	=	=	ND
Liu et al., 2012, summer	Sheep	SF ₆	Forage consisted of dry cornstalk, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	+	=	=	ND
Liu et al., 2012, summer	Sheep	SF ₆	Forage consisted of cornstalk silage, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	=	=	=	ND
Liu et al., 2012, summer	Sheep	SF ₆	Forage consisted of dry cornstalk, ad libitum. F:C ratio 80:20 vs. 60:40 on DM basis	+	=	-	ND
Jonker et al., 2016b	Sheep	RC	Forage consisted of alfalfa silage, 2% of BW. F:C ratio: 100:0 vs. 75:25 vs. 50:50 vs. 35:65	=	+	+	+

¹Where +, -, and = refer to increase ($P < 0.10$), decrease ($P > 0.10$), and no difference ($P > 0.10$), respectively, between the 2 most extreme dietary treatments.

²Methane production in g, L or MJ per day; methane yield in g, L or MJ per kg of DMI; methane energy as % of gross energy intake; methane intensity in g, L or MJ per kg of product (e.g., milk yield and BW gain).

³Not determined.

⁴Herbage consisted of approximately 40% perennial ryegrass, 40% rough stalk meadow grass, 10% annual meadow grass, and 10% white clover.

⁵Linear effect.

⁶Quadratic effect.

⁷Organic matter intake in kg/d.

Table 5. The effect of feed additives (tannin extracts and 3-nitrooxypropanol) on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Tannin extract								
Grainger et al., 2009	Dairy cattle	SF ₆ -tracer technique (SF ₆)	24:76 ^d	Perennial ryegrass supplemented with <i>Acacia mearnsii</i> extract, 35 to 40 kg of DM/cow; 0 vs. 163 g of condensed tannins (CT)/d vs. 266 g of CT/d	=	-	ND ⁵	ND
Duval et al., 2016	Dairy cattle	Respiratory chamber (RC)	54:46	Alfalfa silage and corn silage with quebracho and chestnut extracts, ad libitum; 0 vs. 0.45 vs. 1.8% CT on DM basis with 45 d on diet	=	+	+	ND
Duval et al., 2016	Dairy cattle	RC	54:46	Alfalfa silage and corn silage with quebracho and chestnut extracts, ad libitum; 0 vs. 0.45 vs. 1.8% CT on DM basis with 90 d on diet	=	-	-	ND
Beauchemin et al., 2007	Beef cattle	RC	70:30	Barley silage with 0 vs. 1 vs. 2% red quebracho (<i>Schinopsis quebracho-colorado</i>) extract on DM basis, ad libitum	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 5 mo	RC	54:46 ^e	Corn silage supplemented with <i>A. mearnsii</i> extract, ad libitum; 0 vs. 3% CT/d	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 9 mo	RC	71:29 ^f	Corn silage supplemented with <i>A. mearnsii</i> extract, ad libitum; 0 vs. 3% CT/d	=	-	-	ND
Staerfl et al., 2012	Beef cattle, 11 mo	RC	70:30 ^g	Corn silage supplemented with <i>A. mearnsii</i> extract, ad libitum; 0 vs. 3% CT/d	=	-	-	ND
Śliwiński et al., 2002	Sheep	RC	60:40	Chopped hay with 0 vs. 1 vs. 2 g/kg of DM chestnut tree (<i>Castanea sativa</i>) wood extract, 1.0 × ME	=	=	ND	ND
Carulla et al., 2005	Sheep	RC	100:0	Perennial ryegrass, perennial ryegrass/red clover, perennial ryegrass/alfalfa with 0 vs. 41 g/kg of DM <i>A. mearnsii</i> extract, ad libitum	+	-	-	ND
Hess et al., 2006, experiment 2	Sheep	RC	100:0	Perennial ryegrass supplemented with <i>A. mearnsii</i> extract, 75 g of forage DM/kg of BW ^{0.75} ; 0 vs. 25 g/kg of dietary DM	=	ND	ND	ND
Hess et al., 2006, experiment 2	Sheep	RC	100:0	Perennial ryegrass and red clover (1:1) supplemented with <i>A. mearnsii</i> extract, 75 g of forage DM/kg of BW ^{0.75} ; 0 vs. 25 g/kg of dietary DM	=	ND	ND	ND
Hess et al., 2006, experiment 2	Sheep	RC	100:0	Perennial ryegrass and alfalfa (1:1) supplemented with <i>A. mearnsii</i> extract, 75 g of forage DM/kg of BW ^{0.75} ; 0 vs. 25 g/kg of dietary DM	=	ND	ND	ND
Patra et al., 2011	Sheep	RC	50:50	Wheat straw and concentrate supplemented with seed pulp of <i>Terminalia chebula</i> , ad libitum; 0 vs. 1% of DMI on fresh basis	=	=	=	ND
3-Nitrooxypropanol								
Haisan et al., 2014	Dairy cattle	SF ₆	38:62	Barley silage-based diet supplemented with 3-nitrooxypropanol (3NOP), ad libitum; 0 vs. 2,500 mg/d	=	-	-	ND
Reynolds et al., 2014	Dairy cattle	RC	51:49	Corn silage-based diet with 3NOP administered directly into the rumen; 0 vs. 500 vs. 2,500 mg/d	=	-	-	=
Haisan et al., 2017	Dairy cattle	SF ₆	60:40	Barley silage-based diet supplemented with 3NOP, ad libitum; 0 vs. 1,250 vs. 2,500 mg/d	=	-	-	-
Hristov et al., 2015	Dairy cattle	GreenFeed (GF) + SF ₆	60:40	Corn silage and alfalfa haylage-based diet supplemented with 3NOP, ad libitum; 0 vs. 40 vs. 80 mg/kg of DM	=	- ⁹	- ⁹	- ¹⁰
Lopes et al., 2016	Dairy cattle	GF	55:45	Corn silage- and alfalfa haylage-based diet supplemented with 3NOP, NE _L and MP requirements; 0 vs. 60 mg/kg of DM	=	-	-	ND
Romero-Perez et al., 2014	Beef cattle	RC	60:40	Barley silage-based diet supplemented with 3NOP, restricted; 0 vs. 0.75 vs. 2.25 vs. 4.50 mg/kg of BW per day	=	- ¹¹	- ¹¹	ND
Romero-Perez et al., 2015	Beef cattle	RC	60:40	Barley silage-based diet supplemented with 3NOP, restricted; 0 vs. 2 g/d	=	-	-	ND

Continued

Table 5 (Continued). The effect of feed additives (tannin extracts and 3-nitrooxypropanol) on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	CH ₄ emissions ³				
					DMI (kg/d)	Production	Yield	Energy Intensity	
Vyas et al., 2018	Beef cattle	RC	65:25	High forage diet: barley silage-based diet supplemented with 3NOP, 1.0-kg daily gain; 0 vs. 50 vs. 75 vs. 100 vs. 150 vs. 200 mg/kg of DM	=	- ¹¹	- ¹¹	- ¹¹	ND
Vyas et al., 2018	Beef cattle	RC	8:92	High grain diet: concentrate-based diet supplemented with 3NOP, 2.0-kg daily gain; 0 vs. 50 vs. 75 vs. 100 vs. 150 vs. 200 mg/kg of DM	=	- ¹¹	- ¹¹	- ¹¹	ND
Vyas et al., 2016	Beef cattle	RC	70:30	High forage diet: barley silage-based diet supplemented with 3NOP, 1.0-kg daily gain; 0 vs. 100 vs. 200 mg/kg of DM	=	-	-	-	ND
Vyas et al., 2016	Beef cattle	RC	8:92	High grain diet: concentrate silage-based diet supplemented with 3NOP, 2.0-kg daily gain; 0 vs. 100 vs. 200 mg/kg of DM	=	-	-	-	ND
Martinez-Fernández et al., 2014, experiment 3	Sheep	RC	60:40	Alfalfa hay-based diet supplemented with 3-NOP, 1.1 × ME; 0 vs. 100 mg/d	=	=	-	-	ND

¹Where +, -, and = refer to increase ($P < 0.10$), decrease ($P < 0.10$) and no difference ($P > 0.10$), respectively, between the 2 most extreme dietary treatments.

²Forage to concentrate ratio.

³Methane production in g, L or MJ per day; methane yield in g, L or MJ per kg of DMI; methane energy as % of gross energy intake; methane intensity in g, L or MJ per kg of product (e.g., milk yield and BW gain).

⁴Free access to pasture supplemented with 4.5 kg of DM/d cracked triticale grain. This resulted in forage content in the diet ranging from 23 to 25%.

⁵Not determined.

⁶Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 53 to 56%.

⁷Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 71 to 72%.

⁸Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 69 to 70%.

⁹Quadratic effect was observed when using GF to measure CH₄ emissions, whereas linear effect was observed when using SF₆.

¹⁰Quadratic effect observed when using both GF and SF₆ to measure CH₄ emissions.

¹¹Linear effect.

Table 6. The effect of feed additives (nitrate and garlic) on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³			
						Production	Yield	Energy	Intensity
Nitrate									
Van Zijderveld et al., 2011a ⁴	Dairy cattle	Respiratory chamber (RC)	66:34	Corn silage-based diet supplemented with nitrate, restricted; 0 vs. 21 g/kg of DM	=	-	-	-	-
Lund et al., 2014 ⁵	Dairy cattle	RC	58:42	Grass/clover silage and corn silage supplemented with nitrate for 24 h, ad libitum; 0 vs. 20 g/kg of DM	-	-	-	ND ⁶	ND
Veneman et al., 2015, experiment 1 ⁴	Dairy cattle	RC	80:20	Corn silage and lucerne chaff-based diet supplemented with nitrate, ad libitum; 0 vs. 2% on DM basis	=	-	-	ND	-
Veneman et al., 2015, experiment 2 ⁴	Dairy cattle	RC	60:40	Corn silage and grass silage TMR supplemented with nitrate, ad libitum; 0 vs. 2% on DM basis	-	-	-	ND	=
Klop et al., 2016 ⁴	Dairy cattle	RC	70:30	Mixed ration of grass silage and corn silage supplemented with nitrate, restricted; 0 vs. 21 g/kg of DM	-	-	-	-	-
Olijhoek et al., 2016 ⁴	Dairy cattle	RC	50:50	Corn silage-based TMR supplemented with calcium ammonium nitrate, ad libitum; 0 vs. 5.3 vs. 13.6 vs. 21.1 g of nitrate/kg of DM	=	- ⁷	- ⁷	- ⁷	- ⁷
Newbold et al., 2014, experiment 1 ⁴	Dairy cattle	RC	65:35	Corn silage-based TMR supplemented with nitrate, ad libitum; 0 vs. 0.6 vs. 1.2 vs. 1.8 vs. 2.4 vs. 3% on DM basis	=	- ⁷	- ⁷	ND	ND
Guyader et al., 2015a ⁴	Dairy cattle ⁸	RC	50:50	Natural grassland hay supplemented with calcium nitrate (75% nitrate in product DM), restricted; 0 vs. 3% calcium nitrate on DM basis	-	-	-	-	ND
Guyader et al., 2015b ⁴	Dairy cattle ⁸	RC	50:50	Natural grassland hay supplemented with calcium nitrate (75% nitrate in product DM), restricted; 0 vs. 3% calcium nitrate on DM basis	=	-	-	-	ND
Velazco et al., 2014 ⁴	Beef cattle	GreenFeed	30:70 ⁹	Rolled barley and hay-based diet supplemented with calcium nitrate, ad libitum; 0 vs. 2.57% calcium nitrate on DM basis	-	-	+	ND	=
Hulshof et al., 2012 ⁴	Beef cattle	SF ₆ -tracer technique (SF ₆)	60:40	Freshly chopped sugarcane supplemented with calcium nitrate (75% nitrate in product DM), ad libitum; 0 vs. 22 g of nitrate/kg of DM	-	-	-	-	ND
Lee et al., 2015 ⁴	Beef cattle	RC	55:45	Barley silage and grass hay supplemented with encapsulated nitrate, 1.05-kg daily gain; 0.2 vs. 0.9 vs. 1.9 vs. 2.5% on DM basis	- ¹⁰	- ¹⁰	- ⁷	- ⁷	ND
Lee et al., 2017 ⁴	Beef cattle	RC	65:35	Corn silage supplemented with encapsulated nitrate (nitrate: 0.2 vs. 1.2 vs. 2.3% of diet DM), 1.0-kg daily gain	=	-	=	ND	ND
Lee et al., 2017 ⁴	Beef cattle	RC	65:35	Corn silage supplemented with unencapsulated nitrate (nitrate: 0.2 vs. 2.4% of diet DM), 1.0 kg/d daily gain	=	-	=	ND	ND
Tomkins et al., 2016	Beef cattle	RC	100:0	Flinders grass hay-based diet, replacing urea with calcium nitrate, ad libitum; 0 vs. 4.6 vs. 7.9 g of nitrate/kg of DM	=	-	-	ND	ND
Troy et al., 2015	Beef cattle	RC	50:50	Whole-crop barley silage and grass silage-based TMR supplemented with calcium nitrate, ad libitum; 0 vs. 21.5 g of nitrate/kg of DM	=	-	-	-	ND
Troy et al., 2015	Beef cattle	RC	8:92	Barley and rapeseed meal-based diet supplemented with calcium nitrate, ad libitum; 0 vs. 21.5 g of nitrate/kg of DM	=	-	=	=	ND
Van Zijderveld et al., 2010 ⁴	Sheep	RC	90:10	Corn silage-based diet supplemented with nitrate source, restricted; 0 vs. 2.6% nitrate on DM basis	=	-	-	ND	ND
Nolan et al., 2010 ¹	Sheep	RC	100:0	Chaffed oaten hay supplemented with potassium nitrate, 1 kg/d air-dry feed; 0 vs. 4% potassium nitrate on DM basis	=	-	ND	ND	ND
De Raphélis-Soissan et al., 2014 ⁴	Sheep	RC	100:0	Oaten chaff-based diet, replacing urea with nitrate, 1.3 × ME; 1.1% urea vs. 2% nitrate on a DM basis	-	-	-	ND	ND
El-Zaiat et al., 2014 ⁴	Sheep	RC	60:40	Tifton 85 hay, replacing urea with nitrate, ad libitum; 1.5% urea vs. 4.5% encapsulated nitrate on a DM basis (60.83% nitrate in product DM)	=	-	-	ND	ND

Continued

Table 6 (Continued). The effect of feed additives (nitrate and garlic) on methane (CH₄) emissions of dairy cattle, beef cattle, and sheep¹

Study	Ruminant type	Method of CH ₄ measurements	F:C ²	Dietary treatments and feed allowance	DMI (kg/d)	CH ₄ emissions ³		
						Production	Yield	Intensity
Nguyen et al., 2016	Sheep, faunated	RC	100:0	Oaten chaff-based diet supplemented with calcium nitrate, restricted; 0 vs. 3.1% calcium nitrate on DM basis	+	+	-	ND
Nguyen et al., 2016	Sheep, defaunated	RC	100:0	Oaten chaff-based diet supplemented with calcium nitrate, restricted; 0 vs. 3.1% calcium nitrate on DM basis	+	+	+	ND
Van Zijderveld et al., 2011b, experiment 1	Dairy cattle	RC	66:34	Grass silage and corn silage TMR supplemented with diallyl disulfide (main component garlic oil), restricted; 0 vs. 56 mg/kg of DM	=	=	=	=
Van Zijderveld et al., 2011b, experiment 2	Dairy cattle	RC	76:24	Grass silage and corn silage TMR supplemented with diallyl disulfide (main component garlic oil), restricted; 0 vs. 200 mg/kg of DM	=	=	=	=
Staerfl et al., 2012	Beef cattle, 5 mo	RC	57:43 ¹¹	Corn silage supplemented with dried garlic bulbs, ad libitum; 0 vs. 1.5% of daily DMI	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 9 mo	RC	72:28 ¹²	Corn silage supplemented with dried garlic bulbs, ad libitum; 0 vs. 1.5% of daily DMI	=	=	=	ND
Staerfl et al., 2012	Beef cattle, 11 mo	RC	71:29 ¹³	Corn silage supplemented with dried garlic bulbs, ad libitum; 0 vs. 1.5% of daily DMI	=	=	=	ND
Patra et al., 2011	Sheep	RC	50:50	Wheat straw and concentrate supplemented with seed pulp of <i>Allium sativum</i> , ad libitum; 0 vs. 1% of DMI on fresh basis	=	=	=	=
Van Klevenhusen et al., 2011a	Sheep	RC	49:51	Hay and concentrate diet supplemented with garlic oil, 1.2 × NE _L ; 0 vs. 5 g/kg of DM	=	=	=	ND
Van Klevenhusen et al., 2011a	Sheep	RC	49:51	Hay and concentrate diet supplemented with diallyl disulfide (main component garlic oil), 1.2 × NE _L ; 0 vs. 2 g/kg of DM	=	=	=	ND
Van Klevenhusen et al., 2011b	Sheep	RC	48:52	Meadow hay and concentrate diet supplemented with diallyl disulfide (main component garlic oil), 1.2 × NE _L ; 0 vs. 4 g/kg of DM	=	=	=	ND
Ma et al., 2016	Sheep	RC	12:88	Pelleted TMR and Chinese wild rye hay with garlic extract (allicin), 1,700 g/d; 0 vs. 2 g/head per day	=	=	ND	ND

¹Where +, -, and = refer to increase ($P < 0.10$), decrease ($P < 0.10$), and no difference ($P > 0.10$), respectively, between the 2 most extreme dietary treatments.

²Forage to concentrate ratio.

³Methane production in g, L or MJ per day; methane yield in g, L or MJ per kg of DMI; methane energy as % of gross energy intake; methane intensity in g, L or MJ per kg of product (e.g., milk yield and BW gain).

⁴Iso-nitrogenous: urea was as alternative NPN source to nitrate in the control diet.

⁵There was no adaptation period before methane emissions were measured.

⁶Not determined.

⁷Linear effect.

⁸Nonlactating Holstein cows.

⁹Average F:C ratio; the F:C ratio ranged from 50:50 for the starter diet to 11:89 for the final diet.

¹⁰Quadratic effect.

¹¹Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 56 to 58%.

¹²Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet of approximately 72%.

¹³Bulls received grass silage or corn silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg of DM per bull per day during fattening. This resulted in the forage content in the diet ranging from 70 to 72%.

the effectiveness of increased grass (silage or herbage) or corn silage digestibly on CH₄ emissions. The results for dairy cattle agree with the general assumption that forages containing a smaller concentration of structural carbohydrates, a characteristic associated with higher OMD, may result in decreased CH₄ yield (g/kg of DMI or as % of GEI) due to a shorter MRT of the feed in the rumen (Moe and Tyrrell, 1979), faster fermentation, and a trend toward increased propionate production (Pacheco et al., 2014; van Lingen et al., 2016). According to the work of Blaxter and Clapperton (1965), this inverse relationship between diet digestibility and CH₄ production is valid at feeding levels of 3 times maintenance or more. Upon feeding at maintenance level, a positive linear relationship was found between diet digestibility and CH₄ production. The latter relationship is in line with the findings of Pelchen and Peters (1998). With feed intake levels of sheep ranging from 0.8 × ME to 1.4 × ME, those authors reported increased daily CH₄ production (g/d) when OMD of the ration increased up to approximately 72% digestibility, but not when OMD increased further. Additionally, Moss et al. (1995) found a positive linear relationship between OMD and CH₄ yield (as % of GEI) for sheep fed at 1.2 times maintenance. When sheep were fed at 1.6 times maintenance, Moss et al. (1995) reported an increase in CH₄ yield (% of GEI) up to an OMD of 78%, at which point any further increase in OMD resulted in a decrease in CH₄ yield (% of GEI). Overall, the above-mentioned studies support the findings in the present study for sheep, where increased CH₄ yield was observed with increased OMD.

The observed difference in the effect of increased forage quality on CH₄ emission across the different types of ruminants is most likely related to the differences in feed intake relative to BW. The average increase in DMI relative to BW is largest for dairy cattle, resulting in increased ruminal fermentation and subsequently increased H₂ production and concentration that, by thermodynamic control of NADH oxidation, will drive end products of fermentation toward greater propionate production (van Lingen et al., 2016). This also occurs in beef cattle, but the observed increase in DMI relative to BW might be too small to change ruminal fermentation, H₂ production, and propionate production. Sheep have a relatively low feed intake, which is also not affected by increased forage quality. This results in a relatively low and unaffected H₂ concentration, and no trend toward elevated propionate production. Additionally, as stated earlier, cattle appear to digest low- to medium-quality forages to a greater extent than sheep due to the longer ruminal MRT, whereas the apparent total-tract digestibility of high-quality forages is more similar between these ruminant types. This means that

an increase in forage quality increases ruminal fermentation relatively more in sheep than in cattle, resulting in relatively more CH₄ production, unless a shift toward H₂ sinks (i.e., propionate production) occurs. As suggested above, the latter does not seem to be the case for sheep.

Different Types of Forages

Corn Silage. Table 2 summarizes the studies that have investigated the effect of partially or completely replacing grass pasture, grass silage, or alfalfa silage with corn silage on CH₄ emission from dairy cattle, beef cattle, and sheep. In dairy cattle, increased levels of corn silage resulted in increased DMI and CH₄ production (11 and 8%, respectively), whereas CH₄ emissions generally decreased [CH₄ yield (g/kg of DMI) 5%, CH₄ yield (% of GEI) 7%, and CH₄ intensity (g/kg of milk) 8%]. This dietary strategy did not affect CH₄ emission to the same extent in beef cattle; DMI generally decreased 5% with increased levels of corn silage, with CH₄ production (g/d) following the same trend, and with CH₄ yield (g/kg of DMI) being unaffected. It should be noted that a critical level of dietary starch concentration appears to be required in order for this strategy to be effective in mitigating CH₄ emissions from dairy or beef cattle. This is based on the quadratic responses between dietary corn silage level and CH₄ emissions reported for dairy cattle (Hassanat et al., 2013; van Gastelen et al., 2015) as well as for beef cattle (Jonker et al., 2016b). Only 2 studies were available to investigate the effect of this dietary strategy on CH₄ emissions from sheep, and CH₄ emissions in these studies were largely unaffected by changes in dietary corn silage inclusion. The effectiveness of replacing various forage types with corn silage in reducing CH₄ emissions appears to differ between dairy cattle and beef cattle. Although the results show that increasing corn silage at the expense of another forage is an effective strategy to mitigate CH₄ emissions and stimulate feed intake for dairy cattle, effects observed for beef cattle are less clear. Studies on dairy and beef cattle included in the current analysis were balanced across these ruminant types with regard to the number of studies employing ad libitum or restricted feeding, as well as to those feeding diets with and without concentrate. Therefore, the difference between dairy and beef cattle in the effectiveness of reducing CH₄ emissions by replacing various forage types by corn silage is likely not due to differences in feed allowance or presence of concentrate in the diet, but is instead due to the different response in DMI and apparent total-tract digestibility between these ruminant types. For dairy cattle, the increase in DMI observed with this strategy likely results in increased

ruminal fermentation, and subsequently increased H₂ production and concentration, driving end products of fermentation toward more propionate production (van Lingen et al., 2016). Additionally, if the dietary starch level is above a certain threshold (described previously), fermentation of starch favors ruminal production of propionate at the expense of acetate and decreases rumen pH, which reduces H₂ availability and activity of rumen methanogens even further (Van Kessel and Russell, 1996; Hook et al., 2011). The latter process also applies to beef cattle, but the decrease in DMI (and subsequently ruminal fermentation) might have counterbalanced this effect.

Legumes. Table 3 summarizes the studies investigating the effect of increased levels of dietary legumes on CH₄ emissions from dairy cattle, beef cattle, and sheep. This section focuses only on legumes with negligible concentrations of condensed tannins (alfalfa and clover). Condensed tannins in, for example, birdsfoot trefoil and sainfoin, will be discussed in more detail in the following section. Increased levels of legumes at the expense of grass pasture or grass silage for dairy cattle resulted in increased DMI and CH₄ production (16% and 9%, respectively), whereas CH₄ yield decreased [CH₄ yield (g/kg of DMI) 17%, CH₄ yield (% of GEI) 18%] and CH₄ intensity (g/kg of milk) was unaffected. This strategy did not affect CH₄ emission to the same extent in sheep; DMI generally decreased 5%, with CH₄ production following the same trend, but CH₄ yield in g/kg of DMI and as % of GEI increased slightly by 2%. Only 1 study was available that investigated the effect of this dietary strategy on CH₄ emissions from beef cattle. In this single study, the strategy resulted in increased DMI and CH₄ production and decreased CH₄ yield (% of GEI), which is qualitatively in line with dairy cattle.

These results indicate that the CH₄-mitigating potential of legumes is effective in dairy cattle but not in sheep. In contrast to the dairy cattle studies describing ad libitum feeding, the sheep studies mostly involved restricted feeding. Hammond et al. (2013) offered feeds at fixed maintenance levels to sheep, and Carulla et al. (2005) suggested that the limited excess of feed offered to sheep in their study might have been insufficient to allow the full expression of potentially different voluntary feed intake. Lower feed intake of sheep when fed legumes may have led to an increase in CH₄ yield, therefore masking a potential decline in CH₄ emissions due to replacement of grass by legumes. Contrary to differences in feed allowance between dairy cattle and sheep (i.e., ad libitum vs. restricted, as described above), the F:C ratio was 100:0 in almost all studies (with the exception of Enriquez-Hidalgo et al., 2014) for both dairy cattle and sheep, and therefore does not explain

the differences found in the effectiveness of legumes on CH₄ mitigation between dairy cattle and sheep.

Tannin-Rich Forages. Table 3 summarizes the studies investigating the effect of increased levels of tannin-rich forages (in general; not one particular type) on CH₄ emissions from dairy cattle, beef cattle, and sheep. In dairy cattle, increased levels of tannin-rich forages increased DMI 20%, whereas CH₄ production (g/d) remained unaffected, and CH₄ yield (g/kg of DMI or % of GEI) and, if available, CH₄ intensity (g/kg of milk) decreased 16, 11, and 18%, respectively. Similar to dairy cattle, DMI increased 34% for sheep, whereas CH₄ production remained unaffected and CH₄ yield (g/kg DMI and % of GEI) decreased 23 and 36%, respectively. Only 1 study investigated the effect of this dietary strategy on CH₄ emissions from beef cattle and, in that study, no significant changes in CH₄ emission were reported.

These results indicate that substituting grass pasture or grass silage partially or completely with tannin-rich forages decreases CH₄ emissions from both dairy cattle and sheep. The CH₄-mitigating effect of condensed tannins, especially when combined with grass herbage or silage, might be related to a decrease in digestibility of nutrients, and subsequently H₂ formation and methanogenesis (Jayanegara et al., 2012), as well as toxicity properties suppressing both ruminal protozoa and methanogens (Tavendale et al., 2005; Bhatta et al., 2009).

Forage to Concentrate Ratio

Table 4 summarizes the studies investigating the effect of increased levels of concentrates in the diet at the expense of forage on CH₄ emissions from dairy cattle, beef cattle, and sheep. Increased levels of concentrates increased DMI in cattle (19% for dairy and 23% for beef) but not in sheep, where CH₄ production (g/d) generally followed the same trend, with the exception of beef cattle where CH₄ production decreased 7%. Methane yield (g/kg of DMI) generally decreased for all ruminants (6% for sheep, 14% for dairy cattle, and 26% for beef cattle) as well as CH₄ intensity (g/kg of product; i.e., milk yield for dairy, ADG for beef and sheep; 10% for sheep, 27% for dairy cattle, and 31% for beef cattle). Only CH₄ yield (as % of GEI) produced contrasting results, increasing 19% for sheep but decreasing 12 and 32% for dairy and beef cattle, respectively. The results suggest that an increasing level of concentrates is, despite differences in the feeding allowance (i.e., ad libitum feeding for dairy cattle vs. mainly restricted feeding for beef cattle and sheep), an effective CH₄ mitigation strategy for dairy cattle, beef cattle, and sheep.

Feed Additives

Tannins. Table 5 summarizes the studies investigating the effect of feeding tannin-rich extracts on CH₄ emissions from dairy cattle, beef cattle, and sheep. Only 2 studies each were available to investigate the effect of this dietary strategy on CH₄ emissions from dairy and beef cattle, and effects on CH₄ emissions in those studies were not consistent. For sheep, DMI and daily CH₄ production (g/d) were unaffected, whereas CH₄ yield (g/kg of DMI) was decreased 13%. These results indicate that tannin-rich extracts are an effective CH₄ mitigation strategy for sheep. More research is required to determine the effectiveness for dairy and beef cattle, although the results of the limited number of studies appear to be promising.

3-Nitrooxypropanol. Table 5 summarizes the studies investigating the effect of feeding 3-nitrooxypropanol (3NOP) on CH₄ emissions from dairy cattle, beef cattle, and sheep. Dry matter intake was not affected, whereas CH₄ emissions expressed in any unit considered decreased; CH₄ production (g/d) and CH₄ yield (g/kg of DMI) (35% for dairy cattle and 50% for beef cattle for both units of CH₄ emission), CH₄ yield (as % of GEI; 41% for dairy cattle and 43% for beef cattle), and CH₄ intensity (g/kg of milk; 25% for dairy cattle). Only 1 study investigated the effect of 3NOP on CH₄ emissions in sheep, and found that DMI and CH₄ production were not affected and CH₄ yield (g/kg of DM) decreased upon 3NOP supply. These results illustrate that 3NOP is an effective CH₄-mitigating feed additive for both dairy cattle and beef cattle, despite dairy cattle being mainly fed ad libitum and beef cattle being fed restricted. This is most likely because the mode of action of 3NOP is directly related to methanogenesis (Duin et al., 2016), a process that is similar across ruminant types. In a recent meta-analysis, Dijkstra et al. (2018) concluded that 3NOP indeed reduced CH₄ production and yield in both dairy and beef cattle, but that the antimethanogenic effect of 3NOP was stronger in dairy cattle than in beef cattle when corrected for 3NOP dose and dietary NDF level.

Nitrate. Table 6 summarizes the studies investigating the effect of feeding nitrate on CH₄ emissions from dairy cattle, beef cattle, and sheep. Dry matter intake was generally not affected for dairy cattle and sheep, whereas DMI decreased 4% in beef cattle. Decreases in CH₄ production (g/d; 22% for dairy, 18% for beef, and 28% for sheep), CH₄ yield (g/kg of DMI; 22% for dairy, 12% for beef, and 26% for sheep), CH₄ yield (as % of GEI; 22% for dairy and 14% for beef), and CH₄ intensity (g/kg of product; 20% for dairy) were consistent across ruminant types. Nitrate reduction is

energetically more favorable than methanogenesis (Ungerfeld and Kohn, 2006), and the presence of nitrate in the rumen redirects H₂ from methanogenesis to nitrate reduction, thereby decreasing CH₄ emission (Allison and Reddy, 1984). Approximately the same proportion of the theoretical CH₄ reduction potential of nitrate was reached for dairy cattle (72%), beef cattle (72%), and sheep (74%), indicating that the same amount of nitrate was reduced to ammonia across different types of ruminants.

Garlic. Garlic oil is known to possess antimicrobial properties and has been shown to decrease CH₄ production in vitro (García-Martínez et al., 2005; Chaves et al., 2008). This also applies to the main component of garlic oil; namely, diallyl disulfide (Busquet et al., 2005). Despite the great potential demonstrated in vitro, none of the in vivo studies in the present overview found a CH₄-mitigating effect when feeding garlic, or any of its components, to dairy cattle, beef cattle, or sheep (Table 6). Given these consistent results across ruminant types, we conclude that garlic is an ineffective strategy to reduce CH₄ emission.

CONCLUSIONS

The effectiveness of forage-related CH₄ mitigation strategies, including feeding grass (herbage or silage) with increased levels of digestibility or replacing different forage types with corn silage, differs across dairy cattle, beef cattle, and sheep. These strategies are most effective for dairy cattle, are effective to some extent for beef cattle, but have no or minor effects in sheep. This is most likely due to differences in feed intake level and rumen physiology between the different types of ruminants. In general, the effectiveness of other dietary CH₄ mitigation strategies, including increased concentrate feeding and the use of feed additives (e.g., nitrate), appears to be similar for dairy cattle, beef cattle, and sheep. This illustrates that the modes of action of these strategies are independent of differences in feed intake, rumen physiology, and fermentation characteristics across ruminant types. Therefore, we conclude that if the mode of action of a dietary CH₄ mitigation strategy is directly associated with methanogenesis-related fermentation pathways, the strategy is more likely to have a similar effect across different types of ruminants. If the mode of action of a dietary CH₄ mitigation strategy is related to ruminant-specific factors such as feed intake or rumen physiology, the effectiveness of the strategy is more likely to differ between ruminant types. Subsequently, reductions in CH₄ emission obtained in one type of ruminant may not apply to other ruminant types, as observed in the present study.

ACKNOWLEDGMENTS

The authors acknowledge Kelly Nichols (Wagenin-gen, the Netherlands) for assistance in editing the manuscript for the correct use of English. Authors acknowledge the project “Low Emission Animal Feed” (BO-12.02-009-004), which received financial support of the Dutch Ministry of Economic Affairs (The Hague, the Netherlands), Product Board Animal Feed (Zoetermeer, the Netherlands), and the Dutch Dairy Board (Zoetermeer, the Netherlands). The authors also acknowledge the financial support Sanne van Gastelen and André Bannink received from the Dutch Ministry of Agriculture, Nature and Food Quality (PPS project AF-EU-18010) and The Netherlands Organisation for Scientific Research (ALW.GAS.2) under the ERA-NET Cofund scheme ERAGAS (CEDERS project).

REFERENCES

- Aerts, J. V., J. L. De Boever, B. G. Cottyn, D. L. De Brabander, and F. X. Buysse. 1984. Comparative digestibility of feedstuffs by sheep and cows. *Anim. Feed Sci. Technol.* 12:47–56.
- Aguerre, M. J., M. A. Wattiaux, J. M. Powell, G. A. Broderick, and C. Arndt. 2011. Effect of forage-to-concentrate ratio in dairy cow diets on emission of methane, carbon dioxide, and ammonia, lactation performance, and manure excretion. *J. Dairy Sci.* 94:3081–3093.
- Alexander, R. A., J. F. Hentges Jr., J. T. McCall, and W. O. Ash. 1962. Comparative digestibility of nutrients in roughages by cattle and sheep. *J. Anim. Sci.* 21:373–376.
- Allison, M. J., and C. A. Reddy. 1984. Adaptations of gastrointestinal bacteria in response to changes in dietary oxalate and nitrate. Pages 248–256 in *Current Perspectives in Microbial Ecology: Proceedings of the Third International Symposium of Microbial Ecology*, Washington, DC. M. J. Klug and C. A. Reddy, ed. American Society for Microbiology, Washington, DC.
- Amaral, G. A., D. B. David, J. I. Gere, J. V. Savian, M. M. Kohmann, L. B. Nadin, F. Sánchez Chopa, C. Bayer, and P. C. F. Carvalho. 2016. Methane emissions from sheep grazing pearl millet (*Penisetum americanum* (L.) Leeke) swards fertilized with increasing nitrogen levels. *Small Rumin. Res.* 141:118–123.
- Archimède, H., M. Rira, D. J. Barde, F. Labirin, C. Marie-Magdeleine, B. Calif, F. Periacarpin, J. Fleury, Y. Rochette, D. P. Morgavi, and M. Doreau. 2016. Potential of tannin-rich plants, *Leucaena leucocephala*, *Glyricidia sepium* and *Manihot esculenta*, to reduce enteric methane emissions in sheep. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 100:1149–1158.
- Armstrong, D. G. 1964. Evaluation of artificially dried grasses as a source of energy for sheep. *J. Agric. Sci.* 62:399–416.
- Arndt, C., J. M. Powell, M. J. Aguerre, and M. A. Wattiaux. 2015. Performance, digestion, nitrogen balance, and emission of manure ammonia, enteric methane, and carbon dioxide in lactating cows fed diets with varying alfalfa silage-to-corn silage ratios. *J. Dairy Sci.* 98:418–430.
- Beauchemin, K. A., and S. M. McGinn. 2005. Methane emissions from feedlot cattle fed barley or corn diets. *J. Anim. Sci.* 83:653–661.
- Beauchemin, K. A., S. M. McGinn, T. F. Martinez, and T. A. McAllister. 2007. Use of condensed tannin extract from quebracho trees to reduce methane emissions from cattle. *J. Anim. Sci.* 85:1990–1996.
- Benchaar, C., F. Hassanat, R. Gervais, P. Y. Chouinard, H. V. Petit, and D. I. Massé. 2014. Methane production, digestion, ruminal fermentation, nitrogen balance, and milk production of cows fed corn silage- or barley silage-based diets. *J. Dairy Sci.* 97:961–974.
- Bhatta, R., Y. Uyeno, K. Tajima, A. Takenaka, Y. Yabumoto, I. Nonaka, O. Enishi, and M. Kurihara. 2009. 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.* 92:5512–5522.
- Blaxter, K. L., and J. L. Clapperton. 1965. Prediction of the amount of methane produced by ruminants. *Br. J. Nutr.* 19:511–522.
- Blaxter, K. L., and F. W. Wainman. 1961. The utilization of food by sheep and cattle. *J. Agric. Sci.* 57:419–425.
- Blaxter, K. L., F. W. Wainman, and J. L. Davidson. 1966. The voluntary intake of food by sheep and cattle in relation to their energy requirements for maintenance. *Anim. Prod.* 8:75–83.
- Boadi, D. A., and K. M. Wittenberg. 2002. Methane production from dairy and beef heifers fed forages differing in nutrient density using the sulphur hexafluoride (SF₆) tracer gas technique. *Can. J. Anim. Sci.* 82:201–206.
- Brask, M., P. Lund, A. L. F. Hellwing, M. Poulsen, and M. R. Weisbjerg. 2013. Enteric methane production, digestibility and rumen fermentation in dairy cows fed different forages with and without rapeseed fat supplementation. *Anim. Feed Sci. Technol.* 184:67–79.
- Busquet, M., S. Calsamiglia, A. Ferret, M. D. Carro, and C. Kamel. 2005. Effect of garlic oil and four of its compounds on rumen microbial fermentation. *J. Dairy Sci.* 88:4393–4404.
- Cammell, S. B., J. D. Sutton, D. E. Beever, D. J. Humphries, and R. H. Phipps. 2000. The effect of crop maturity on the nutritional value of maize silage for lactating dairy cows 1. Energy and nitrogen utilization. *Anim. Sci.* 71:381–390.
- Carulla, J. E., M. Kreuzer, A. Machmüller, and H. D. Hess. 2005. Supplementation of *Acacia mearnsii* tannins decreases methanogenesis and urinary nitrogen in forage-fed sheep. *Aust. J. Agric. Res.* 56:961–970.
- Chaves, A. V., M. L. He, W. Z. Yang, A. N. Hristov, T. A. McAllister, and C. Benchaar. 2008. Effects of essential oils on proteolytic, deaminative and methanogenic activities of mixed ruminal bacteria. *Can. J. Anim. Sci.* 88:117–122.
- Colucci, P. E., G. K. Macleod, W. L. Grovum, L. W. Cahill, and I. McMillan. 1989. Comparative digestion in sheep and cattle fed different forage to concentrate ratios at high and low intakes. *J. Dairy Sci.* 72:1774–1785.
- Colucci, P. E., G. K. Macleod, W. L. Grovum, I. McMillan, and D. J. Barney. 1990. Digesta kinetics in sheep and cattle fed diets with different forage to concentrate ratios at high and low intakes. *J. Dairy Sci.* 73:2143–2156.
- De Oliveira, S. G., T. T. Berchielli, M. dos Santos Pedreira, O. Primavesi, R. Prighetto, and M. A. Lima. 2007. Effect of tannin levels in sorghum silage and concentrate supplementation on apparent digestibility and methane emission in beef cattle. *Anim. Feed Sci. Technol.* 135:236–248.
- De Raphélis-Soissan, V., L. Li, I. R. Godwin, M. C. Barnett, H. B. Perdok, and R. S. Hegarty. 2014. Use of nitrate and *Propionibacterium acidipropionici* to reduce methane emissions and increase wool growth of Merino sheep. *Anim. Prod. Sci.* 54:1860–1866.
- Delgado, D. C., J. Galindo, J. Cairo, I. Orta, M. Dominquez, and N. Dorta. 2013. Supplementation with foliage of *L. leucocephala*. Its effect on the apparent digestibility of nutrients and methane production in sheep. *Cuban J. Agric. Sci.* 47:267–271.
- Dijkstra, J., A. Bannink, J. France, E. Kebreab, and S. van Gastelen. 2018. Short communication: Antimethanogenic effects of 3-nitrooxypropanol depend on supplementation dose, dietary fiber content, and cattle type. *J. Dairy Sci.* 101:9041–9047.
- Dini, Y., J. I. Gere, C. Cajarville, and V. S. Ciganda. 2017. Using highly nutritious pastures to mitigate enteric methane emissions from cattle grazing systems in South America. *Anim. Prod. Sci.* <https://doi.org/10.1071/AN16803>.
- Doreau, M., A. Ferlay, Y. Rochette, and C. Martin. 2014. Effects of dehydrated lucerne and soya bean meal on milk production and composition, nutrient digestion, and methane and nitrogen losses in dairy cows receiving two different forages. *Animal* 8:420–430.
- Doreau, M., H. M. G. van der Werf, D. Micol, H. Dubroeuq, J. Agabriel, Y. Rochette, and C. Martin. 2011. Enteric methane production and greenhouse gases balance of diets differing in concentrate in the fattening phase of a beef production system. *J. Anim. Sci.* 89:2518–2528.

- Duin, E. C., T. Wagner, S. Shima, D. Prakash, B. Cronin, D. R. Yáñez-Ruiz, S. Duval, R. Rumbeli, R. T. Stemmler, R. K. Thauer, and M. Kindermann. 2016. Mode of action uncovered for the specific reduction of methane emissions from ruminants by the small molecule 3-nitrooxypropanol. *Proc. Natl. Acad. Sci. USA* 113:6172–6177.
- Duval, B. D., M. Aguerre, M. Wattiaux, P. A. Vadas, and J. M. Powell. 2016. Potential for reducing on-farm greenhouse gas and ammonia emissions from dairy cows with prolonged dietary tannin additions. *Water Air Soil Pollut.* 227:329.
- El-Zaiat, H. M., R. C. Araujo, Y. A. Soltan, A. S. Morsy, H. Louvandini, A. V. Pires, H. O. Patino, P. S. Correa, and A. L. Abdalla. 2014. Encapsulated nitrate and cashew nut shell liquid on blood and rumen constituents, methane emission, and growth performance of lambs. *J. Anim. Sci.* 92:2214–2224.
- Enriquez-Hidalgo, D., T. Gilliland, M. H. Deighton, M. O'Donovan, and D. Hennessy. 2014. Milk production and enteric methane emissions by dairy cows grazing fertilized perennial ryegrass pasture with or without inclusion of white clover. *J. Dairy Sci.* 97:1400–1412.
- Ferris, C. P., F. J. Gordon, D. C. Patterson, M. G. Porter, and T. Yan. 1999. The effect of genetic merit and concentrate proportion in the diet on nutrient utilization by lactating dairy cows. *J. Agric. Sci.* 132:483–490.
- Fievez, V., F. Piattoni, L. Mbanzambihigo, and D. Demeyer. 1999. Reductive acetogenesis in the hindgut and attempts to its induction in the rumen—A review. *J. Appl. Anim. Res.* 16:1–22.
- García-Martínez, R., M. J. Ranilla, M. L. Tejido, and M. D. Carro. 2005. Effects of disodium fumarate on *in vitro* rumen microbial growth, methane production and fermentation of diets differing in their forage:concentrate ratio. *Br. J. Nutr.* 94:71–77.
- Gerber, P. J., A. Mottet, C. I. Opio, A. Falcucci, and F. Teillard. 2015. Environmental impacts of beef production: Review of challenges and perspectives for durability. *Meat Sci.* 109:2–12.
- Goopy, J. P., A. Donaldson, R. Hegarty, P. E. Vercoe, F. Haynes, M. Barnett, and V. H. Oddy. 2014. Low-methane yield sheep have smaller rumens and shorter rumen retention time. *Br. J. Nutr.* 111:578–585.
- Gordon, F. J., M. G. Porter, C. S. Maybe, E. F. Unsworth, and D. J. Kilpatrick. 1995. Effect of forage digestibility and type of concentrate on nutrient utilization by lactating dairy cattle. *J. Dairy Res.* 62:15–27.
- Grainger, C., T. Clarke, M. J. Auldist, K. A. Beauchemin, S. M. McGinn, G. C. Waghorn, and R. J. Eckard. 2009. Potential use of *Acacia mearnsii* condensed tannins to reduce methane emissions and nitrogen excretion from grazing dairy cows. *Can. J. Anim. Sci.* 89:241–251.
- Grovum, W. L., and V. J. Williams. 1977. Rate of passage of digesta in sheep. 6. The effect of level of food intake on mathematical predictions of the kinetics of digesta in the reticulorumen and intestines. *Br. J. Nutr.* 38:425–436.
- Günal, M., A. McCourt, Y. Zhao, Z. G. Yan, and T. Yan. 2018. The effect of silage type on animal performance, energy utilisation and enteric methane emission in lactating dairy cows. *Anim. Prod. Sci.* <https://doi.org/10.1071/AN16435>.
- Guyader, J., M. Eugène, M. Doreau, D. P. Morgavi, C. Gérard, C. Loncke, and C. Martin. 2015a. Nitrate but not tea saponin feed additives decreased enteric methane emissions in nonlactating cows. *J. Anim. Sci.* 93:5367–5377.
- Guyader, J., M. Eugène, B. Meunier, M. Doreau, D. P. Morgavi, M. Silberberg, Y. Rochette, C. Gérard, C. Loncke, and C. Martin. 2015b. Additive methane-mitigating effect between linseed oil and nitrate fed to cattle. *J. Anim. Sci.* 93:3564–3577.
- Haisan, J., Y. Sun, L. Guan, K. A. Beauchemin, A. Iwaasa, S. Duval, M. Kindermann, D. R. Barreda, and M. Oba. 2017. The effects of feeding 3-nitrooxypropanol at two doses on milk production, rumen fermentation, plasma metabolites, nutrient digestibility, and methane emissions in lactating Holstein cows. *Anim. Prod. Sci.* 57:282–289.
- Haisan, J., Y. Sun, L. L. Guan, K. A. Beauchemin, A. Iwaasa, S. Duval, D. R. Barreda, and M. Oba. 2014. The effects of feeding 3-nitrooxypropanol on methane emissions and productivity of Holstein cows in mid lactation. *J. Dairy Sci.* 97:3110–3119.
- Hammond, K. J., J. L. Burke, J. P. Koolaard, S. Muetzel, C. S. Pinares-Patiño, and G. C. Waghorn. 2013. Effects of feed intake on enteric methane emissions from sheep fed fresh white clover (*Trifolium repens*) and perennial ryegrass (*Lolium perenne*) forages. *Anim. Feed Sci. Technol.* 179:121–132.
- Hart, K. J., P. G. Martin, P. A. Foley, D. A. Kenny, and T. M. Boland. 2009. Effect of sward dry matter digestibility on methane production, ruminal fermentation, and microbial populations of zero-grazed beef cattle. *J. Anim. Sci.* 87:3342–3350.
- Hassanat, F., R. Gervais, C. Julien, D. I. Massé, A. Lettat, P. Y. Chouinard, H. V. Petit, and C. Benchaar. 2013. Replacing alfalfa silage with corn silage in dairy cow diets: Effects on enteric methane production, ruminal fermentation, digestion, N balance, and milk production. *J. Dairy Sci.* 96:4553–4567.
- Hatew, B., A. Bannink, H. van Laar, L. H. de Jonge, and J. Dijkstra. 2016. Increasing harvest maturity of whole-plant corn silage reduces methane emission of lactating dairy cows. *J. Dairy Sci.* 99:354–368.
- Henderson, G., F. Cox, S. Ganesh, A. Jonker, W. YoungGlobal Rumen Census Collaborators, and P. H. Janssen. 2015. Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. *Sci. Rep.* 5:14567.
- Hess, H. D., T. T. Tiemann, F. Noto, J. E. Carulla, and M. Kreuzer. 2006. Strategic use of tannins as means to limit methane emission from ruminant livestock. *Int. Congr. Ser.* 1293:164–167.
- Hindrichsen, I. K., H.-R. Wettstein, A. Machmüller, and M. Kreuzer. 2006. Methane emission, nutrient degradation and nitrogen turnover in dairy cows and their slurry at different milk production scenarios with and without concentrate supplementation. *Agric. Ecosyst. Environ.* 113:150–161.
- Hook, S. E., M. Steele, K. Northwood, A.-D. Wright, and B. McBride. 2011. Impact of high-concentrate feeding and low ruminal pH on methanogens and protozoa in the rumen of dairy cows. *Microb. Ecol.* 62:94–105.
- Hristov, A. N., J. Oh, J. L. Firkins, J. Dijkstra, E. Kebreab, G. Waghorn, H. P. S. Makkar, A. T. Adesogan, W. Yang, C. Lee, P. J. Gerber, B. Henderson, and J. M. Tricarico. 2013a. Mitigation of methane and nitrous oxide emissions from animal operations: I. A review of enteric methane mitigation options. *J. Anim. Sci.* 91:5045–5069.
- Hristov, A. N., J. Oh, F. Giallongo, T. W. Frederick, M. T. Harper, H. L. Weeks, A. F. Branco, P. J. Moate, M. H. Deighton, S. R. Williams, M. Kindermann, and S. Duval. 2015. Use of 3-nitrooxypropanol as feed additive for mitigating enteric methane emissions from ruminants: a meta-analysis. *Proc. Natl. Acad. Sci. USA* 112:10663–10668.
- Hristov, A. N., T. Ott, J. Tricarico, A. Rotz, G. Waghorn, A. Adesogan, J. Dijkstra, F. Montes, J. Oh, E. Kebreab, S. J. Oosting, P. J. Gerber, B. Henderson, H. P. S. Makkar, and J. L. Firkins. 2013b. Mitigation of methane and nitrous oxide emissions from animal operations: III. A review of animal management mitigation options. *J. Anim. Sci.* 91:5095–5113.
- Hulshof, R. B. A., A. Berndt, W. J. J. Gerrits, J. Dijkstra, S. M. van Zijderveld, J. R. Newbold, and H. R. Perdok. 2012. Dietary nitrate supplementation reduces methane emission in beef cattle fed sugarcane-based diets. *J. Anim. Sci.* 90:2317–2323.
- Huyen, N. T., O. Desrues, S. J. J. Alferink, T. Zandstra, M. W. A. Verstegen, W. H. Hendriks, and W. F. Pelikaan. 2016. Inclusion of sainfoin (*Onobrychis viciifolia*) silage in dairy cow rations affects nutrient digestibility, nitrogen utilization, energy balance and methane emissions. *J. Dairy Sci.* 99:3566–3577.
- Jayanegara, A., F. Leiber, and M. Kreuzer. 2012. Meta-analysis of the relationship between dietary tannin level and methane formation in ruminants from *in vivo* and *in vitro* experiments. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 96:365–375.
- Jeyanathan, J., M. Kirs, R. S. Ronimus, S. O. Hoskin, and P. J. Janssen. 2011. Methanogen community structure in the rumens of

- farmed sheep: cattle and red deer fed different diets. *FEMS Microbiol. Ecol.* 76:311–326.
- Jonker, A., K. Lowe, S. Kittelman, P. H. Janssen, S. Ledgard, and D. Pacheco. 2016b. Methane emissions changed nonlinearly with graded substitution of alfalfa silage with corn silage and corn grain in the diet of sheep and relation with rumen fermentation characteristics *in vivo* and *in vitro*. *J. Anim. Sci.* 94:3464–3475.
- Jonker, A., S. Muetzel, G. Molano, and D. Pacheco. 2016a. Effect of fresh pasture quality, feeding level and supplementation on methane emissions from growing beef cattle. *Anim. Prod. Sci.* 56:1714–1721.
- Klop, G., B. Hatew, A. Bannink, and J. Dijkstra. 2016. Feeding nitrate and docosahexaenoic acid affects enteric methane production and milk fatty acid composition in lactating dairy cows. *J. Dairy Sci.* 99:1161–1172.
- Lage, J. F., E. San Vito, R. A. Reis, E. E. Dallantonia, L. R. Simonetti, I. P. C. Carvalho, A. Berndt, M. L. Chizzotti, R. T. S. Friguetto, and T. T. Berchielli. 2016. Methane emissions and growth performance of young Nelore bulls fed crude glycerine- v. fibre-based energy ingredients in low or high concentrate diets. *J. Agric. Sci.* 154:1280–1290.
- Leaver, J. D., R. C. Campling, and W. Holmes. 1969. The effect of level of feeding on the digestibility of diets for sheep and cattle. *Anim. Sci.* 11:11–18.
- Lechner-Doll, M., M. Kaske, and W. van Engelhardt. 1991. Factors affecting the mean retention time of particles in the forestomach of ruminants and camelids. Pages 455–482 in *Physiological Aspects of Digestion and Metabolism of Ruminants: Proc. 7th Int. Symp. Ruminant Physiology*. T. Tsuda, Y. Sasaki, and R. Kawashima, ed. Academic Press Inc., San Diego, CA.
- Lee, C., R. C. Araujo, K. M. Koenig, and K. A. Beauchemin. 2015. Effects of encapsulated nitrate on enteric methane production and nitrogen and energy utilization in beef heifers. *J. Anim. Sci.* 93:2391–2404.
- Lee, C., R. C. Araujo, K. M. Koenig, and K. A. Beauchemin. 2017. Effects of encapsulated nitrate on growth performance, nitrate toxicity, and enteric methane emissions in beef steers: Backgrounding phase. *J. Anim. Sci.* 95:3700–3711.
- Lee, J. M., S. L. Woodward, G. C. Waghorn, and D. A. Clark. 2004. Methane emissions by dairy cows fed increasing proportions of white clover (*Trifolium repens*) in pasture. *Proc. N.Z. Grassland Assoc.* 66:151–155.
- Lindberg, J. E. 1985. Estimation of rumen degradability of feed proteins with the sacco technique and various *in vitro* methods: A review. *Acta Agric. Scand. Suppl.* 25:64–79.
- Lindberg, J. E. 1988. Retention times of small feed particles and of water in the gut of dairy goats fed at different levels of intake. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 59:173–181.
- Liu, C., Z. P. Zhu, B. Shang, Y. X. Chen, T. J. Guo, Y. M. Luo, and H. M. Dong. 2012. Effects of dietary types or concentrate-to-forage ratios on rumen methane emissions of sheep. ILES12-0599 in *Proc. IX International Livestock Environment Symposium (ILES IX)*, Valencia, Spain. American Society of Agricultural and Biological Engineers, St. Joseph, MI.
- Lopes, J. C., L. F. de Matos, M. T. Harper, F. Giallongo, J. Oh, D. Gruen, S. Ono, M. Kindermann, S. Duval, and A. N. Hristov. 2016. Effect of 3-nitrooxypropanol on methane and hydrogen emissions, methane isotopic signature, and ruminal fermentation in dairy cows. *J. Dairy Sci.* 99:5335–5344.
- Lovett, D., S. Lovell, L. Stack, J. Callan, M. Finlay, J. Conolly, and F. P. O'Mara. 2003. Effect of forage/concentrate ratio and dietary coconut oil level on methane output and performance of finishing beef heifers. *Livest. Prod. Sci.* 84:135–146.
- Lovett, D. K., L. J. Stack, S. Lovell, J. Callan, B. Flynn, M. Hawkins, and F. P. O'Mara. 2005. Manipulating enteric methane emissions and animal performance of late-lactation dairy cows through concentrate supplementation at pasture. *J. Dairy Sci.* 88:2836–2842.
- Lund, P., R. Dahl, H. J. Yng, A. L. F. Hellwing, B. B. Cao, and M. R. Weisbjerg. 2014. The acute effect of addition of nitrate on *in vitro* and *in vivo* methane emission in dairy cows. *Anim. Prod. Sci.* 54:1432–1435.
- Ma, T., D. Chen, Y. Tu, N. Zhang, B. Si, K. Deng, and Q. Diao. 2016. Effect of supplementation of allicin on methanogenesis and ruminal microbial flora in Dorper crossbred ewes. *J. Anim. Sci. Biotechnol.* 7:1.
- Margan, D. E., J. B. Moran, and F. B. Spence. 1994. Energy and protein value of combinations of maize silage and red clover hay for ruminants, using adult sheep as a model. *Aust. J. Exp. Agric.* 34:319–329.
- Martin, C., D. P. Morgavi, and M. Doreau. 2010. Methane mitigation in ruminants: From microbe to the farm scale. *Animal* 4:351–365.
- Martínez-Fernández, G., L. Abecia, A. Arco, G. Cantalapiedra-Hijar, A. I. Martín-García, E. Molina-Alcaide, M. Kindermann, S. Duval, and D. R. Yáñez-Ruiz. 2014. Effects of ethyl-3-nitrooxy propionate and 3-nitrooxypropanol on ruminal fermentation, microbial abundance, and methane emissions in sheep. *J. Dairy Sci.* 97:3790–3799.
- Mc Geough, E. J., P. O'Kiely, P. A. Foley, K. J. Hart, T. M. Boland, and D. A. Kenny. 2010a. Methane emissions, feed intake, and performance of finishing beef cattle offered maize silages harvested at 4 different stages of maturity. *J. Anim. Sci.* 88:1479–1491.
- Mc Geough, E. J., P. O'Kiely, K. J. Hart, A. P. Moloney, T. M. Boland, and D. A. Kenny. 2010b. Methane emissions, feed intake, performance, digestibility, and rumen fermentation of finishing beef cattle offered whole-crop wheat silages differing in grain content. *J. Anim. Sci.* 88:2703–2716.
- McAllister, T. A., and C. J. Newbold. 2008. Redirecting rumen fermentation to reduce methanogenesis. *Aust. J. Exp. Agric.* 48:7–13.
- McCaughey, W. P., K. Wittenberg, and D. Corrigan. 1999. Impact of pasture type on methane production by lactating beef cows. *Can. J. Anim. Sci.* 79:221–226.
- McCourt, A. R., T. Yan, and C. S. Mayne. 2007. Effect of forage type on methane production from dairy cows. Page 048 in *Proc. Br. Soc. Anim. Sci.*, Southport, UK. Cambridge University Press, Cambridge, UK.
- McDonald, P., R. A. Edwards, J. F. D. Greenhalgh, and C. A. Morgan. 2002. *Animal Nutrition*. Pearson Prentice Hall, Harlow, UK.
- Moe, P. W., and H. F. Tyrrell. 1979. Methane production in dairy cows. *J. Dairy Sci.* 62:1583–1586.
- Molano, G., and H. Clark. 2008. The effect of level of intake and forage quality on methane production by sheep. *Aust. J. Exp. Agric.* 48:219–222.
- Moss, A. R., D. I. Givens, and P. C. Garnworthy. 1995. The effect of supplementing grass silage with barley on digestibility, *in sacco* degradability, rumen fermentation and methane production in sheep at two levels of intake. *Anim. Feed Sci. Technol.* 55:9–33.
- Murray, R. M., A. M. Bryant, and R. A. Leng. 1976. Rates of production of methane in the rumen and large intestine of sheep. *Br. J. Nutr.* 36:1–14.
- Newbold, J. R., S. M. van Zijderveld, R. B. A. Hulshof, W. B. Fokkink, R. A. Leng, P. Terencio, W. J. Powers, P. S. J. van Adrichem, N. D. Paton, and H. R. Perdok. 2014. The effect of incremental levels of dietary nitrate on methane emissions in Holstein steers and performance in Nelore bulls. *J. Anim. Sci.* 92:5032–5040.
- Nguyen, S. H., M. C. Barnett, and R. S. Hegarty. 2016. Use of dietary nitrate to increase productivity and reduce methane production of defaunated and faunated lambs consuming protein-deficient chaff. *Anim. Prod. Sci.* 56:290–297.
- Nocek, J. E. 1988. *In situ* and other methods to estimate ruminal protein and energy digestibility: A review. *J. Dairy Sci.* 71:2051–2069.
- Nolan, J. V., R. S. Hegarty, J. Hegarty, I. R. Godwin, and R. Woodgate. 2010. Effects of dietary nitrate on fermentation, methane production and digesta kinetics in sheep. *Anim. Prod. Sci.* 50:801–806.
- Norton, B. W., H. Pieris, and R. Elliott. 1994. Fermentation pattern and diet utilization by cattle, sheep and goats given grain or molasses based diets. *Proc. Australas. Soc. Anim. Prod.* 20:182–185.
- Okine, E. K., G. W. Mathison, and R. T. Hardin. 1989. Effects of changes in frequency of reticular contractions on fluid and particulate passage rates in cattle. *J. Anim. Sci.* 67:3388–3396.
- Olijhoek, D. W., A. L. F. Hellwing, M. Brask, M. R. Weisbjerg, O. Højberg, M. K. Larsen, J. Dijkstra, E. J. Erlandsen, and P. Lund. 2016. Effect of dietary nitrate level on enteric methane production,

- hydrogen emission, rumen fermentation, and nutrient digestibility in dairy cows. *J. Dairy Sci.* 99:6191–6205.
- Pacheco, D., G. Waghorn, and P. H. Janssen. 2014. Decreasing methane emissions from ruminants grazing forages: A fit with productive and financial realities? *Anim. Prod. Sci.* 54:1141–1154.
- Patra, A. K., D. N. Kamra, R. Bhar, R. Kumar, and N. Agarwal. 2011. Effect of *Terminalia chebula* and *Allium sativum* on *in vivo* methane emission by sheep. *J. Anim. Physiol. Anim. Nutr. (Berl.)* 95:187–191.
- Pearson, R. A., R. F. Archibald, and R. H. Muirhead. 2006. A comparison of the effect of forage type and level of feeding on the digestibility and gastrointestinal mean retention time of dry forages given to cattle, sheep, ponies and donkeys. *Br. J. Nutr.* 95:88–98.
- Pelchen, A., and K. J. Peters. 1998. Methane emissions from sheep. *Small Rumin. Res.* 27:137–150.
- Pinares-Patiño, C. S., R. Baumont, and C. Martin. 2003. Methane emissions by Charolais cows grazing a monospecific pasture of timothy at four stages of maturity. *Can. J. Anim. Sci.* 83:769–777.
- Poppi, D. P., D. J. Minson, and J. H. Ternouth. 1980. Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. *Aust. J. Agric. Res.* 32:99.
- Poppi, D. P., D. J. Minson, and J. H. Ternouth. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. 11. Factors controlling the retention of feed in the reticulo-rumen. *Aust. J. Agric. Res.* 32:109–121.
- Potts, S. B., M. Shaughnessy, and R. A. Erdman. 2017. The decline in digestive efficiency of US dairy cows from 1970 to 2014. *J. Dairy Sci.* 100:5400–5410.
- Prigge, E. C., M. J. Baker, and G. A. Varga. 1984. Comparative digestion rumen fermentation and kinetics of forage diets by steers and wethers. *J. Anim. Sci.* 59:237–245.
- Rees, M. C., and D. A. Little. 1980. Differences between sheep and cattle in digestibility, voluntary intake and retention time in the rumen of three tropical grasses. *J. Agric. Sci. (Camb.)* 94:483–485.
- Reid, R. L., G. A. Jung, J. M. Cox-Ganser, B. F. Rybeck, and E. C. Townsend. 1990. Comparative utilization of warm- and cool-season forages by cattle, sheep and goats. *J. Anim. Sci.* 68:2986–2994.
- Reynolds, C. K., L. A. Crompton, J. A. N. Mills, D. J. Humphries, P. Kirton, A. E. Relling, T. H. Misselbrook, D. R. Chadwick, and D. I. Givens. 2010. Effects of diet protein level and forage source on energy and nitrogen balance and methane and nitrogen excretion in lactating dairy cows. Pages 463–464 in *Proc. 3rd EAAP International Symposium on Energy and Protein Metabolism and Nutrition*. G. M. Crovetto, ed. Wageningen Academic Publishers, Parma, Italy.
- Reynolds, C. K., D. J. Humphries, P. Kirton, M. Kindermann, S. Duval, and W. Steinberg. 2014. Effects of 3-nitrooxypropanol on methane emission, digestion, and energy and nitrogen balance of lactating dairy cows. *J. Dairy Sci.* 97:3777–3789.
- Romero-Perez, A., E. K. Okine, S. M. McGinn, L. L. Guan, M. Oba, S. M. Duval, M. Kindermann, and K. A. Beauchemin. 2014. The potential of 3-nitrooxypropanol to lower enteric methane emissions from beef cattle. *J. Anim. Sci.* 92:4682–4693.
- Romero-Perez, A., E. K. Okine, S. M. McGinn, L. L. Guan, M. Oba, S. M. Duval, M. Kindermann, and K. A. Beauchemin. 2015. Sustained reduction in methane production from long-term addition of 3-nitrooxypropanol to a beef cattle diet. *J. Anim. Sci.* 93:1780–1791.
- Šebek, L. B. J., and H. Everts. 1999. *In situ* rumen degradation of dry matter and crude protein in ewes and dairy cows. *Anim. Sci.* 68:801–808.
- Siddons, R. C., and J. Paradine. 1983. Protein degradation in the rumen of sheep and cattle. *J. Sci. Food. Agric.* 4:701–708.
- Śliwiński, B. J., M. Kreuzer, H.-R. Wettstein, and A. Machmüller. 2002. Rumen fermentation and nitrogen balance of lambs fed diets containing plant extracts rich in tannins and saponins, and associated emissions of nitrogen and methane. *Arch. Tierernähr.* 56:379–392.
- Soto-Navarro, S. A., R. Lopez, C. Sankey, B. M. Capitan, B. P. Holland, L. A. Balstad, and C. R. Krehbiel. 2014. Comparative digestibility by cattle versus sheep: Effect of forage quality. *J. Anim. Sci.* 92:1621–1629.
- Staerfl, S. M., J. O. Zeitz, M. Kreuzer, and C. R. Soliva. 2012. Methane conversion rate of bulls fattened on grass or maize silage as compared with the IPCC default values, and the long-term methane mitigation efficiency of adding acacia tannin, garlic, maca and lupine. *Agric. Ecosyst. Environ.* 148:111–120.
- Südekum, K.-H., H. Röh, M. Brandt, G. Rave, and M. Strangassinger. 1995. Comparative digestion in cattle and sheep fed wheat silage diets at low and high intakes. *J. Dairy Sci.* 78:1498–1511.
- Swainson, N. M., S. O. Hoskin, H. Clark, C. S. Pinares-Patiño, and I. M. Brookes. 2008. Comparative methane emissions from cattle, red deer and sheep. *Proc. N.Z. Soc. Anim. Prod.* 68:59–62.
- Tavendale, M. H., L. P. Meagher, D. Pacheco, N. Walker, G. T. Attwood, and S. Sivakumaran. 2005. 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.* 123–124:403–419.
- Tiemann, T. T., C. E. Lascano, H. R. Wettstein, A. C. Mayer, M. Kreuzer, and H. D. Hess. 2008. Effect of the tropical tannin-rich shrub legumes *Calliandra calothyrsus* and *Flemingia macrophylla* on methane emission and nitrogen and energy balance in growing lambs. *Animal* 2:790–799.
- Tomkins, N., A. J. Parker, G. Hepworth, and M. J. Callaghan. 2016. Nitrate supplementation has marginal effects on enteric methane production from *Bos indicus* steers fed Flinders grass (*Iseilema* spp.) hay, but elevates blood methaemoglobin concentrations. *Anim. Prod. Sci.* 58:262–270. <https://doi.org/10.1071/AN16002>.
- Troy, S. M., C.-A. Duthie, J. J. Hyslop, R. Roehle, D. W. Ross, R. J. Wallace, A. Waterhouse, and J. A. Rooke. 2015. Effectiveness of nitrate addition and increased oil content as methane mitigation strategies for beef cattle fed two contrasting basal diets. *J. Anim. Sci.* 93:1815–1823.
- Tyrrell, H. F., and P. W. Moe. 1972. Net energy value for lactation of a high and low concentrate ration containing corn silage. *J. Dairy Sci.* 55:1106–1112.
- Udén, P., and P. J. Van Soest. 1984. Investigations of the *in situ* bag technique and a comparison of the fermentation in heifers, sheep, ponies and rabbits. *J. Anim. Sci.* 58:213–221.
- Ulyatt, M. J., K. R. Lassey, I. D. Shelton, and C. F. Walker. 2002. Seasonal variation in methane emission from dairy cows and breeding ewes grazing ryegrass/white clover pasture in New Zealand. *N. Z. J. Agric. Res.* 45:217–226.
- Ungerfeld, E. M., and R. A. Kohn. 2006. The role of thermodynamics in the control of ruminal fermentation. Pages 55–85 in *Ruminant physiology: Digestion, metabolism and impact of nutrition on gene expression, immunology and stress*. K. Sejrsen, T. Hvelplund, and M. O. Nielsen, ed. Wageningen Academic Publishers, Wageningen, the Netherlands.
- Van Dorland, H. A., H.-R. Wettstein, H. Leuenberger, and M. Kreuzer. 2007. Effect of supplementation of fresh and ensiled clovers to ryegrass on nitrogen loss and methane emission of dairy cows. *Livest. Sci.* 111:57–69.
- van Gastelen, S., E. C. Antunes-Fernandes, K. A. Hettinga, G. Klop, S. J. J. Alferink, W. H. Hendriks, and J. Dijkstra. 2015. Enteric methane production, rumen volatile fatty acid concentrations, and milk fatty acid composition in lactating Holstein-Friesian cows fed grass silage- or corn silage-based diets. *J. Dairy Sci.* 98:1915–1927.
- Van Kessel, J. A. S., and J. B. Russell. 1996. The effect of pH on ruminal methanogenesis. *FEMS Microbiol. Ecol.* 20:205–210.
- Van Klevenhusen, F., J. O. Zeitz, S. Duval, M. Kreuzer, and C. R. Soliva. 2011a. Garlic oil and its principal component diallyl disulfide fail to mitigate methane, but improve digestibility in sheep. *Anim. Feed Sci. Technol.* 166–167:356–363.
- Van Klevenhusen, F., J. O. Zeitz, S. Duval, M. Kreuzer, and C. R. Soliva. 2011b. Diallyl disulfide and lovastatin: Effects on energy and protein utilisation in, as well as methane emission from, sheep. *Arch. Anim. Nutr.* 65:255–266.
- van Lingen, H. J., C. M. Plugge, J. G. Fadel, E. Kebreab, A. Bannink, and J. Dijkstra. 2016. Thermodynamic driving force of hydrogen

- on rumen microbial metabolism: A theoretical investigation. *PLoS One* 11:e0161362.
- van Zijderveld, S. M., J. Dijkstra, H. B. Perdok, J. R. Newbold, and W. J. J. Gerrits. 2011b. Dietary inclusion of diallyl disulfide, yucca powder, calcium fumarate, an extruded linseed product, or medium-chain fatty acids does not affect methane production in lactating dairy cows. *J. Dairy Sci.* 94:3094–3104.
- van Zijderveld, S. M., W. J. J. Gerrits, J. A. Apajalahti, J. R. Newbold, J. Dijkstra, R. A. Leng, and H. B. Perdok. 2010. Nitrate and sulfate: Effective alternative hydrogen sinks for mitigation of ruminal methane production in sheep. *J. Dairy Sci.* 93:5856–5866.
- van Zijderveld, S. M., W. J. J. Gerrits, J. Dijkstra, J. R. Newbold, R. B. A. Hulshof, and H. B. Perdok. 2011a. Persistency of methane mitigation by dietary nitrate supplementation in dairy cows. *J. Dairy Sci.* 94:4028–4038.
- Velazco, J. I., D. J. Cottle, and R. S. Hegarty. 2014. Methane emissions and feeding behaviour of feedlot cattle supplemented with nitrate or urea. *Anim. Prod. Sci.* 54:1737–1740.
- Veneman, J. B., S. Muetzel, K. J. Hart, C. L. Faulkner, J. M. Moorby, H. B. Perdok, and C. J. Newbold. 2015. Does dietary mitigation of enteric methane production affect rumen function and animal productivity in dairy cows? *PLoS One* 10:e0140282.
- Vyas, D., S. M. McGinn, S. M. Duval, M. Kindermann, and K. A. Beauchemin. 2016. Effects of sustained reduction of enteric methane emissions with dietary supplementation of 3-nitrooxypropanol on growth performance of growing and finishing beef cattle. *J. Anim. Sci.* 94:2024–2034.
- Vyas, D., S. M. McGinn, S. M. Duval, M. K. Kindermann, and K. A. Beauchemin. 2018. Optimal dose of 3-nitrooxypropanol for decreasing enteric methane emissions from beef cattle fed high-forage and high-grain diets. *Anim. Prod. Sci.* 58:1049–1055.
- Waldo, D. R., H. F. Tyrrell, A. V. Capuco, and C. E. Rexroad Jr.. 1997. Components of growth in Holstein heifers fed either alfalfa or corn silage diets to produce two daily gains. *J. Dairy Sci.* 80:1674–1684.
- Warner, D., A. Bannink, B. Hatew, H. van Laar, and J. Dijkstra. 2017. Effects of grass silage quality and level of feed intake on enteric methane production in lactating dairy cows. *J. Anim. Sci.* 95:3687–3700.
- Warner, D., B. Hatew, S. C. Podesta, G. Klop, S. van Gastelen, H. van Laar, J. Dijkstra, and A. Bannink. 2016. Effects of nitrogen fertilisation rate and maturity of grass silage on methane emission by lactating dairy cows. *Animal* 10:34–43.
- Warner, D., S. C. Podesta, B. Hatew, G. Klop, H. van Laar, A. Bannink, and J. Dijkstra. 2015. Effect of nitrogen fertilization rate and regrowth interval of grass herbage on methane emission of zero-grazing lactating dairy cows. *J. Dairy Sci.* 98:3383–3393.
- Waugh, C. D., D. A. Clark, G. C. Waghorn, and S. L. Woodward. 2005. Feeding maize silage to dairy cows: Implications for methane emissions. *Proc. N.Z. Soc. Anim. Prod.* 65:356–361.
- Woodward, S. L., G. C. Waghorn, and P. G. Laboyrie. 2004. Condensed tannins in birdsfoot trefoil (*Lotus corniculatus*) reduce methane emissions from dairy cows. *Proc. N.Z. Soc. Anim. Prod.* 64:160–164.
- Woodward, S. L., G. C. Waghorn, M. J. Ulyatt, and K. R. Lassey. 2001. Early indications that feeding *Lotus* will reduce methane emissions from ruminants. *Proc. N.Z. Soc. Anim. Prod.* 61:23–26.