SPECIAL TOPICS—Mitigation of methane and nitrous oxide emissions from animal operations: I. A review of enteric methane mitigation options[1]

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ABSTRACT: The goal of this review was to analyze published data related to mitigation of enteric methane (CH_4) emissions from ruminant animals to document the most effective and sustainable strategies. Increasing forage digestibility and digestible forage intake was one of the major recommended CH_4 mitigation practices. Although responses vary, CH_4 emissions can be reduced when corn silage replaces grass silage in the diet. Feeding legume silages could also lower CH_4 emissions compared to grass silage due to their lower fiber concentration. Dietary lipids can be effective in reducing CH_4 emissions, but their applicability will depend on effects on feed intake, fiber digestibility, production, and milk composition. Inclusion of concentrate feeds in the diet of ruminants will likely decrease CH_4 emission intensity (Ei; CH_4 per unit animal product), particularly when inclusion is above 40% of dietary dry matter and rumen function is not impaired. Supplementation of diets containing medium to poor quality forages with small amounts of concentrate feed will typically decrease CH_4 Ei. Nitrates show promise as CH_4 mitigation agents, but more studies are needed to fully understand their impact on whole-farm greenhouse gas emissions, animal productivity, and animal health. Through their effect on feed efficiency and rumen stoichiometry, ionophores are likely to have a moderate CH_4 mitigating effect in ruminants fed high-grain or mixed grain–forage diets. Tannins may also reduce CH_4 emissions although in some situations intake and milk production may be compromised. Some direct-fed microbials, such as yeast-based products, might have a moderate CH_4–mitigating effect through increasing animal productivity and feed efficiency, but the effect is likely to be inconsistent. Vaccines against rumen archaea may offer mitigation opportunities in the future although the extent of CH_4 reduction is likely to be small and adaptation by ruminal microbes and persistence of the effect is unknown. Overall, improving forage quality and the overall efficiency of dietary nutrient use is an effective way of decreasing CH_4 Ei. Several feed supplements have a potential to reduce CH_4 emission from ruminants although their long-term effect has not been well established and some are toxic or may not be economically feasible.

Key words: enteric methane, mitigation, ruminant animal

INTRODUCTION

The livestock sector represents a significant source of greenhouse gas (**GHG**) emissions worldwide, generating carbon dioxide (**CO_2**), methane (**CH_4**; i.e., enteric CH_4 in this review), and nitrous oxide (**N_2O**) either directly (e.g., from enteric fermentation and manure management) or indirectly (e.g., from feed-production

activities and conversion of forest into pasture). Using a life cycle assessment (**LCA**) approach and accounting for land-use change, Steinfeld et al. (2006) estimated that the livestock sector contributes about 18% of the total global anthropogenic GHG emissions. Based on data by the U.S. Environmental Protection Agency (USEPA, 2006), the direct livestock contribution to non-CO_2 emissions (i.e., CH_4 and N_2O) can be estimated at 7.3 and 7.5% of the global GHG emission values for 2010 and 2020 and can be even lower for some industrialized countries (3.1% of the total U.S. GHG emissions in 2009; USEPA, 2011). Enteric fermentation and manure decomposition, the processes responsible for CH_4 and N_2O emissions, are the main targets of GHG mitigation practices for the livestock industries. Discussions in this review are based on a recent comprehensive review of non-CO_2 GHG mitigation measures for the livestock sector by Hristov et al. (2013b). The second (Montes et al., 2013) and third (Hristov et al., 2013c) papers in this series address CH_4 and N_2O emissions from manure decomposition and animal management-related CH_4 and N_2O mitigation strategies, respectively. Interactions among mitigation practices for individual components of livestock production systems are discussed in Gerber et al. (2013).

ENTERIC METHANE EMISSIONS FROM FARM ANIMALS AND WILD RUMINANTS

Methane and CO_2 are natural by-products of microbial fermentation of carbohydrates and, to a lesser extent, AA in the rumen and the hindgut of farm animals. Methane emissions represent a loss of about 5 to 7% of dietary GE (to as low as 3% in cattle fed high-grain diets) and are about 16 to 26 g/kg of dietary DMI (could be lower with diets containing very high proportions of grain). Sheep and goats produce 10 to 16 kg CH_4/yr and cattle 60 to 160 kg/yr, depending on their size and DMI. Methane is produced in strictly anaerobic conditions by highly specialized methanogenic prokaryotes, all of which are archaea. In ruminants, current techniques estimate that the majority of CH_4 production occurs in the reticulorumen. Rectal emissions account for about 2 to 3% of the total CH_4 emissions in sheep or dairy cows (Murray et al., 1976; Muñoz et al., 2012). As stated by Van Soest (1994), the basic problems in anaerobic metabolism are the storage of oxygen (i.e., as CO_2) and disposal of hydrogen equivalents (i.e., as CH_4). Recently, a new group of methylotrophic methanogens (belonging to the so-called rumen cluster-C group) that does not require hydrogen as an energy source has been described and appears to play a role in CH_4 formation in ruminants (Poulsen et al., 2012).

Domestic nonruminant herbivore animals (horses, donkeys, mules, and hinnies) also produce CH_4 as a result of fermentation processes in their hindgut. Hindgut fermenters, however, do not produce as much CH_4 per unit of fermented feed as ruminants, perhaps as a result of availability of hydrogen sinks other than CH_4 (Jensen, 1996) and lower absolute amounts of CH_4 produced due to digestion of feed in the small intestine before entering the hindgut. The Intergovernmental Panel for Climate Change (**IPCC**, 2006) assumed CH_4 emissions from horses at 18 kg/head per yr (compared with 128 kg/head per yr for a high-producing dairy cow of similar BW).

Wild animals, especially ruminants, also emit CH_4 from enteric fermentation in their reticulorumen or the hindgut (Crutzen et al., 1986; Jensen, 1996; Galbraith et al., 1998; Kelliher and Clark, 2010). The present-day contribution of wild ruminants to the global GHG emissions, however, is relatively low. Current CH_4 emissions from wild ruminants (bison, elk, and deer) for the contiguous United States were estimated at about 6 Tg CO_2–equivalents (**CO_2e**)/yr, or 4.3% of the emissions from domestic ruminants (Hristov, 2012). In contrast, in the presettlement period, wild ruminants emitted from 62 to 154 Tg CO_2e/yr, depending on the assumed size of the bison population, which is on average about 86% of the present-day CH_4 emissions from domestic ruminants in the contiguous United States (Hristov, 2012). Marsupials present a special case. Although their diet is similar to that of ruminants, they reportedly produce little or no CH_4 (Kempton et al., 1976). Recent data by Madsen and Bertelsen (2012), however, reported wallabies produce CH_4 at a rate of about 1.6 to 2.5% of their GE intake (**GEI**), which is about one-third of the expected CH_4 emission from ruminants consuming a similar diet.

Relative to ruminants, monogastric farm animals are minor emitters of CH_4. For example, the IPCC (2006) assumed CH_4 emission factors for pigs at about 1.2 to 2.8% of the emission factors for cattle [1.5 vs. 53 (beef or growing cattle) or 128 kg CH_4/head per yr for a high-producing North American dairy cow]. Recent estimates place total GHG emissions from pigs and poultry at about 9.5 and 9.7%, respectively, of the GHG emissions from livestock (FAO, 2013).

MITIGATION DATABASE

More than 900 publications were selected and reviewed by Hristov et al. (2013b). In analyzing the effects of various mitigation practices on CH_4 emissions, the authors did not account for the effect of these practices in the whole-farm or production cycle context. This task can be accomplished through LCA. The current analysis placed particular emphasis on animal experimentation data, and therefore, LCA were generally excluded. Data generated by rumen-simulation in vitro batch or continuous culture systems were deliberately

excluded. In vitro systems are convenient for screening a large number of treatments, but due to various factors, they lack representativeness of the in vivo rumen (Hristov et al., 2012) and usually do not address the major question of adaptation of the rumen ecosystem to the mitigation practice. The rumen microbes can adapt to some bioactive compounds (saponins, for example) and perhaps not to others (Makkar and Becker, 1997; Wallace et al., 2002). Unfortunately, although scientists are clearly aware of this issue, very few in vivo studies have examined the long-term effect of mitigation agents or practices. Therefore, for most of the CH_4 mitigation practices discussed in this document, data for persistency of the effect are critically needed.

The vast majority of the studies covered in the original review by Hristov et al. (2013b) examined mitigation practices in isolation and rarely discussed potential interactions in the context of the whole production system. This is a significant disadvantage of the mitigation literature because mitigation practices may counteract or be synergistic to each other (del Prado et al., 2010). In the context of the whole-farm GHG emission reductions, it is important that assessments of mitigation practices take into account "pollution swapping," that is, decreasing the emissions of one GHG while increasing another or causing an upstream or downstream increase in the emission of the same GHG.

The metrics used to quantify GHG emissions should accurately reflect the mitigation potential of various practices and should be standardized. Despite documented relationships among digestibility, intake, and CH_4 production (absolute or per unit of DMI), the CH_4 conversion rate factor ($\mathbf{Y_m}$) used by the IPCC (2006) is calculated as CH_4 energy as percent of GEI. Ellis et al. (2010) evaluated 9 empirical CH_4 prediction equations and observed the Y_m factor model to perform adequately, compared with other equations. However, these authors argued that because it is based simply on GEI, Y_m does not have the capacity to fully describe changes in composition of the diet and has limited use when estimating the impact of varying nutritional strategies on CH_4 emissions. For example, the IPCC Y_m model could not decipher between an increase in CH_4 caused by an increase in DMI and a change in CH_4 caused by an increase in the fat content of the diet, which would have differing effects on the resulting CH_4 emission but may not differ in GEI. Thus, the validity of the Y_m approach is questionable, and perhaps CH_4 energy loss should be expressed on a DE basis, which will better reflect forage quality and other mitigation practices, such as grain or fat inclusion in ruminant diets. The term "emission intensity" (**Ei**; in this manuscript, this is CH_4 or total GHG per unit animal product) has been introduced for CH_4 emission (Leslie et al., 2008) and, because it is based on emissions per unit of product, reflects most accurately the effect of a given

mitigation practice on the composite of feed intake, CH_4 emission, and animal productivity.

The accuracy and precision of CH_4 measurement techniques is another important consideration when examining mitigation practices. For example, several publications have reviewed various aspects of measuring CH_4, with particular emphasis on the sulfur hexafluoride ($\mathbf{SF_6}$) technique (Makkar and Vercoe, 2007; Williams et al., 2011; Lassey et al., 2011; Storm et al., 2012). The SF_6 tracer method has been shown to produce larger variability than respiration chambers (Grainger et al., 2007; Hammond et al., 2009; Clark, 2010; Moate et al., 2011), but it enables emissions to be determined in a large number of animals and in free grazing conditions. Novel in vivo approaches, such as the use of CO_2 as a tracer gas (Madsen et al., 2010) and the Green-Feed system (C-Lock, Inc., Rapid City, SD; Huhtanen et al., 2013; Hammond et al., 2013b), have also been proposed. Therefore, when evaluating mitigation practices, it is important to examine critically the measurement methods used, particularly in relation to CH_4 production.

Another critical aspect of all mitigation practices, including those targeting CH_4, that must be considered is their likelihood of adoption. Farmers are unlikely to adopt practices that 1) have no production (i.e., economic) benefit or 2) are not mandatory and/or supported by governmental subsidies. Overall, unrealistic expectations on non-CO_2 GHG emission reductions from the livestock sector must be avoided. In any production system, profitability is often the most important decision-making factor that will determine adoption of any of the mitigation practices. Any practice that requires additional investment without a clear positive economic return or has a chance of decreasing animal productivity or increasing production cost is likely to be rejected by the livestock producer. Therefore, when assessing the mitigation potential of various practices, users must consider the combined effects of interactions among animal–manure–soil–crop processes related to whole-farm profitability, potential effectiveness on farms (vs. experimental results), and the likely adoption rate. Also, further attention is needed to better document variation associated with mitigation practices so that livestock producers can assess uncertainty and risk. It is important to realize, for example, that most ruminants (including beef before entering a feedlot) graze pastures under extensive, low intensity systems, which makes implementation of mitigating strategies very challenging.

MITIGATION OPTIONS

Comprehensive reviews on enteric and manure CH_4 (and N_2O) mitigation technologies and overall farm sustainability have been published (Harris and Kolver, 2001; Boadi et al., 2004; Kebreab et al., 2006; Ellis et al., 2008; Beauchemin et al. 2007b, 2009; Eckard et al.,

2010; Martin et al., 2010; Cottle et al., 2011; Goel and Makkar, 2012; for a full list see Hristov et al., 2013b) and data from these reports have been extensively used in the preparation of this document. A summary of the CH_4 mitigation practices discussed in this manuscript is presented in Table 1.

Inhibitors

Research in this area has targeted chemical compounds with a specific inhibitory effect on rumen archaea. Among the most successful compounds tested in vivo were bromochloromethane (**BCM**), 2-bromo-ethane sulfonate, chloroform, and cyclodextrin. These CH_4 inhibitors reduced CH_4 production by up to 50% in vivo (in sheep, goat and cattle; Immig et al., 1996; Lila et al., 2004; Mitsumori et al., 2011; Knight et al., 2011). Although some studies have suggested adaptation of the rumen ecosystem to this class of compounds (Johnson et al., 1972; Immig et al., 1996), thus reducing their long-term efficacy, the effect of BCM appeared to persist in the studies by Sawyer et al. (1974), Tomkins et al. (2009), and Abecia et al. (2012). Data by Knight et al. (2011) showed an immediate and dramatic drop in CH_4 production in dry cows administered chloroform; however, CH_4 production gradually increased to about 62% of the pretreatment levels by d 42, suggesting adaptation to chloroform by the rumen ecosystem. A banned compound, such as BCM (an ozone-depleting agent), cannot be recommended as a CH_4 mitigating agent, but compounds with similar mode of action could be developed. The long-term effect of CH_4 inhibitors is uncertain and more data are needed to establish their effects on production. In addition, public acceptance (due to perception and/or existing or future regulations or because they are known carcinogens, e.g., chloroform) could be barriers to their adoption. Nevertheless, research groups around the world are working on developing natural or synthetic compounds that directly inhibit rumen methanogenesis. A recent example of these efforts is research with 3-nitro-oxypropanol (**3NP**). The compound decreased CH_4 production per unit of DMI in sheep in respiration chambers (a 24% reduction; Martinez-Fernandez et al., 2013) and dairy cows using the SF_6 technique (a dramatic 60% decrease; Haisan et al., 2013). In another trial with lactating cows, the reduction in CH_4 production was only about 8% and there was no response to a fivefold increase in application rate (from 500 to 2,500 mg/d; Reynolds et al., 2013). The authors, however, observed a sharp decrease in CH_4 production (respiration chambers) immediately after 3NP administration and speculated that the compound may be rapidly absorbed, metabolized, or washed out of the rumen and continuous infusion or feeding may be a more effective method of application.

Electron Receptors

This category of CH_4 mitigating agents has recently received renewed attention. Among these, fumarate, nitrates, sulfates, and nitroethane (Gutierrez-Banuelos et al., 2007; Brown et al., 2011) have been studied the most. Leng (2008) provided a comprehensive review of the earlier literature on nitrates. Recent research with sheep (Sar et al., 2004; Nolan et al., 2010; Van Zijderveld et al., 2010) and cattle (Van Zijderveld et al., 2011b,c; Hulshof et al., 2012) has shown promising results with nitrates decreasing CH_4 production by up to 50%. Potential issues with these compounds include adaptation of the rumen ecosystem, which has not been studied in long-term animal experiments with perhaps one exception from which nitrate persistently decreased CH_4 production from lactating dairy cows during 4 successive 24-d periods (Van Zijderveld et al., 2011c). Additional issues with nitrates include potential increase in ammonia production and potential toxicity from intermediate products (nitrite). The toxicity issue was discussed in detail by Leng (2008) who emphasized the critical importance of gradual adaptation of the animal to nitrate and that low-protein diets are the natural background for successful utilization of nitrates as a CH_4 mitigating tool. If nitrates are provided as a substitute for urea in licking blocks, access to the blocks should be limited so that nitrate intake does not poison the animal. Intake of feed additives through licking blocks or liquid supplements can be extremely variable (Cockwill et al., 2000) and this variability has to be considered when the blocks contain potentially toxic substances such as nitrates. It is important to recognize that the adaptability of the rumen ecosystem to reduce nitrate may be short lived after nitrate withdrawal from the diet (Alaboudi and Jones, 1985). Nitrate level in the basal diet should also be considered when supplemental nitrate is fed. Some loss of supplemental nitrate N with urine is expected (Takahashi et al., 1998), but its effect on total urinary N losses is unclear. In one study, nitrate supplementation did not increase volatile N losses from manure (Van Zijderveld et al., 2011c) although the control diet was supplemented with urea.

Adding sulfate to the diet of sheep also reduced CH_4 production, and when both nitrate and sulfate were added, the effect on CH_4 production was additive (Van Zijderveld et al., 2010). High inclusion of distillers grains in feedlot diets in the United States has triggered intensive research on the effect of high-S diets (also in combination with high-S drinking water) on the occurrence of S-induced polioencephalomalacia (Gould, 2000; Cammack et al., 2010; Schoonmaker and Beitz, 2012), caused by excessive production of hydrogen sulfide in the rumen.

Fumaric and malic acids have also been studied as alternative hydrogen sinks in the rumen (Bayaru et al., 2001;

Table 1. Feed additives and feeding strategies targeting enteric methane (CH_4) emission mitigation

Category[1]	Potential CH_4 mitigating effect[2]	Long-term effect established	Effective[3]	Environmentally safe or safe to the animal[4]	Recommended[5]
Inhibitors					
BCM and BES[6]	High	?[7]	Yes	No[8]	No
Chloroform	High	No?	Yes	No	No
Cyclodextrin	Low	No	Yes	No	No
3-nitrooxypropanol	Medium	?	Yes	?	?
Electron receptors					
FMA[9]	No effect to High	?	?	Yes	No?
Nitroethane	Low	No	Yes?	No	No
Nitrate	High	No?	Yes	?	Yes?[10]
Ionophores[11]	Low[12]	No?	Yes?[12]	Yes?	Yes?
Plant bioactive compounds[13]					
Tannins[14] (condensed)	Low	No?	Yes	Yes	Yes?
Saponins	Low?	No	?	Yes	No?
Essential oils	Low?	No	?	Yes	No
Exogenous enzymes	No effect to Low	No	No?	Yes?	No?
Defaunation	Low	No	?	Yes	No
Manipulation of rumen archaea and bacteria	Low?	No	?	Yes?	Yes?[15]
Dietary lipids	Medium	No?	Yes	Yes	Yes?[16]
Inclusion of concentrate[17]	Low to Medium	Yes	Yes	Yes	Yes?[18]
Improving forage quality	Low to Medium	Yes	Yes	Yes	Yes
Grazing management	Low	Yes	Yes?	Yes	Yes?[19]
Feed processing	Low	Yes	Yes[20]	Yes[20]	Yes[20]
Mixed rations and feeding frequency[21]	?	?	?	Yes	?
Precision (balanced) feeding and feed analysis	Low to Medium	Yes	Yes?	Yes	Yes[22]

[1]Mitigation strategies in this table are applicable to all ruminants.

[2]High, ≥30% mitigating effect; Medium, 10 to 30% mitigating effect; Low, ≤10% mitigating effect. Mitigating effects refer to percent change over a "standard practice" (i.e., study control that was used for comparison) and are based on combination of study data and judgment by the authors of this document.

[3]Effectiveness is determined on the basis of CH_4 mitigation potential, effect on feed intake (no negative effect is beneficial), and/or effect on animal productivity (no negative effect or improvement is beneficial).

[4]Based on available data and authors' expert opinion

[5]Based on available research or lack of sufficient research.

[6]BCM = bromochloromethane; BES = 2-bromo-ethane sulfonate.

[7]? = uncertainty due to limited research or lack of data, inconsistent or variable results, or lack (or insufficient) data on persistency of the effect.

[8]Class I ozone-depleting substance (www.epa.gov/ozone/science/ods/classone.html; EPA, 2013).

[9]FMA = fumaric and malic acids.

[10]Practicality of use is unknown. Caution must be exercised when feeding nitrate. Animal should be properly adapted and re-adapted if nitrate supplementation is discontinued for a period of time. Access to molasses blocks with nitrate should be limited so that nitrate intake does not poison the animal. Unwise to use when diets have high N concentrations.

[11]Most data are for monensin. Monensin does not appear to have a consistent direct effect on CH_4 production in dairy or beef cattle. Meta-analyses have shown improvement in feed efficiency in beef cattle (Goodrich et al., 1984) and dairy cows (Duffield et al., 2008) that may reduce CH_4 emissions per unit of product (meat or milk). On this basis, the overall conclusion is that ionophores likely have a CH_4 mitigating effect in ruminants of up to 5%.

[12]Through improvement in feed efficiency, especially when diets contain concentrates; no effect when pasture is fed as a sole diet.

[13]See text for extensive discussion on these supplements. Tannins appear more effective than saponins. Results with tea saponins are encouraging but must be confirmed and data for persistence of the effect are lacking.

[14]Detrimental effects when dietary CP is marginal or inadequate or when condensed tannins are astringent and in high concentrations, but with adequate dietary CP some condensed tannins can have wide ranging benefits.

[15]Promising, but the technology is not yet developed or commercially available.

[16]Lipids are generally effective in reducing CH_4 production. They are recommended when their use is economically feasible (high-oil by-products of the biofuel industries, for example). Their potential negative effect on feed intake, fiber digestibility, rumen function, milk fat content, and overall animal productivity must be considered. Maximum recommended inclusion rate in ruminant diets is 6 to 7% (total fat) of dietary DM. With the lack of incentive mechanisms to reduce CH_4 emissions, the economic feasibility of supplementing diets with edible lipids is questionable.

[17]Higher rates of concentrate inclusion may decrease intake, but production is usually increased. Negative effects on fiber degradability and milk composition (in dairy cows) must be avoided.

[18]Although recommended (direct reduction in CH4 emission or indirect through increased animal productivity), the applicability of this mitigation practice will heavily depend on feed availability. See text for further discussion.

[19]Not very consistent results, but recommended on the base that improving pasture quality should reduce CH_4 emissions per unit of feed intake and animal product.

[20]Conditionally effective (if fiber degradability is not decreased), safe to the environment (energy input may counteract greenhouse gas mitigating effect; has to be determined using life cycle assessment), and recommended (if economically feasible and does not jeopardize fiber digestibility).

[21]Insufficient data.

[22]Even if direct CH_4 mitigation effect is uncertain, precision (balanced) feeding and accurate feed analyses will likely enhance animal productivity and feed efficiency and improve farm profitability (and thus have an indirect mitigating effect on enteric and manure CH_4 and N_2O emissions).

Molano et al., 2008; Foley et al., 2009; Van Zijderveld et al., 2011a). Their mitigating potential has been questioned (Ungerfeld et al., 2007) because it is generally lower than that of nitrates and results have been inconsistent. In a number of experiments, fumarate addition did not affect CH_4 production (McGinn et al., 2004; Beauchemin and Mc-Ginn, 2006; Kolver and Aspin, 2006; McCourt et al., 2008; Molano et al., 2008; Van Zijderveld et al., 2011a). With the exception of one study (Wood et al., 2009), in which a 76% decrease in CH_4 production was reported 8 wk after the introduction of fumaric acid, with gaseous emissions measured using a tunnel system, the long-term effects of these compounds have not been demonstrated.

Ionophores

Monensin has been the most studied ionophore and it is routinely used in beef production and more recently in dairy cattle nutrition in North America. Ionophores are banned in the European Union even though there is no evidence of genes coding for their resistance as are with other feed-administered antibiotics (Russell and Houlihan, 2003). There have been a number of experiments with monensin as a rumen modifier in various production systems, where CH_4 production was studied as a main objective either from a mitigation or from an energy loss perspective (Sauer et al., 1998; Van Vugt et al., 2005; Waghorn et al., 2008; Grainger et al., 2010$^)$. Although some studies reported a long-term mitigating effect of monensin on CH_4 production (Odongo et al., 2007), overall the effect of the ionophore appears to be inconsistent. In a meta-analysis of 22 controlled studies, monensin (given at 32 mg/kg DM) reduced CH_4 emissions and Y_m in beef steers fed total mixed rations (**TMR**) by 19 ± 4 g/animal per d ($P < 0.001$) and 0.33 ± 16% ($P = 0.047$), respectively (Appuhamy et al., 2013). The corresponding reductions in dairy cows were 6 ± 3 g/animal per d ($P = 0.065$) and 0.23 ± 14% ($P = 0.095$) for monensin given at a dose of 21 mg/kg DM. Overall, the conclusion of that analysis was that monensin had stronger antimethanogenic effect in beef steers than dairy cows (mostly fed forage-based diets), but the effects in dairy cows can be improved by dietary modifications and increasing monensin dose.

Meta-analyses have shown monensin to improve feed efficiency in feedlot cattle (by 7.5%; Goodrich et al., 1984), growing cattle on pasture (by 15%; Potter et al., 1986), and dairy cows (by 2.5%; Duffield et al., 2008), which might lead to reduced CH_4 Ei. A recent meta-analysis by Duffield et al. (2012) reported an average increased in feed efficiency in feedlot cattle due to monensin inclusion of 6.4% but also found the effect decreased from 8.1 in the 1970s to 2.3 and 3.5% in the 1990s and 2000s, respectively (with the decrease attributed to continuously improving management that has resulted in a 27%

increase in feed efficiency). The analysis found a linear effect of monensin dose on feed efficiency and suggested that the expected improvement in modern feedlots should be from 2.5 to 3.5% and will depend on dose and dietary energy. Moreover, another meta-analysis has also shown a consistent decrease in acetate:propionate (**Ac:Pr**) ratio with monensin addition in high grain diets fed to beef cattle (Ellis et al., 2012a), which may lead to a reduction in CH_4 emission per unit of feed.

Plant Bioactive Compounds

This category includes a variety of plant secondary compounds, specifically tannins, saponins, and essential oils and their active ingredients.

Tannins and saponins have been extensively studied and show the most mitigating potential within this category. Tannins, as feed supplements or as tanniferous plants have often, but not always (Beauchemin et al., 2007a), shown a potential for reducing CH_4 emission by up to 20% (Woodward et al., 2001; Sliwinski et al., 2002; Waghorn et al., 2002; Zhou et al., 2011; Staerfl et al., 2012). Condensed (and hydrolyzable) tannins are widely distributed in browse and warm climate forages and are usually considered antinutritional although they can have considerable potential to reduce intestinal nematode numbers and allow acceptable production in the presence of a parasite burden (Niezen et al., 1995, 1998a,b; Terrill et al., 1992).

Tannins will inevitably be antinutritional when dietary CP concentrations are limiting production because they reduce absorption of AA (Waghorn, 2008). Structure, molecular weight (and hence activity), and concentration of tannins affect the nutritive value of the diet. It is important that benefits of reduced CH_4 yields do not overshadow detrimental effects of tannins on digestion and production, as observed by Grainger et al. (2009) with dairy cows on pasture supplemented with grain. In that study, CH_4 emission was reduced by up to 30%, but milk production of the cows was also reduced by about 10%.

A meta-analysis of in vivo experiments with tannins by Jayanegara et al. (2012) reported a relatively close relationship between dietary tannin concentration and CH_4 production per unit of digestible OM. These authors, however, reported a trend ($P = 0.08$) for decreased feed intake and a statistically significant decrease in nutrient digestibility, particularly of CP, with increasing dietary tannin concentration. Reduced digestibility of diets containing condensed tannins at high levels is common (Waghorn, 2008; Patra, 2010) and is unavoidable if urinary N loss is reduced because dietary N is diverted to feces (reducing apparent CP and OM digestibilities). This is an important factor that must be considered when feeding supplemental tannins or tanniferous plants. Tanniferous forages can have beneficial effects on silage quality and ruminant

health due to improved protein supply, bloat safety, and antiparasitic properties (Broderick, 1995; McMahon et al., 2000; Frutos et al., 2004); their recommendation as cattle feed, however, must involve the agronomic characteristics of these species (Waghorn, 2008).

A recent extensive review of the effect of saponins and tannins on CH_4 production in ruminants examined mostly in vivo studies with both plant bioactive compounds (**PBAC**; Goel and Makkar, 2012). The authors concluded that the risk of impaired rumen function and animal productivity with tannins is greater than with saponins and, for decreasing CH_4 production, the concentration range for tannins is narrower than for saponins. In some dietary situations, however, decreased protein degradability in the rumen, combined with a shift in protein digestion to the small intestine, may be beneficial. Such a shift may also have the benefit of reducing urinary N losses (vs. fecal N losses).

According to Goel and Makkar (2012), the antimethanogenic effect of tannins depends on the dietary concentration and is positively related to the number of hydroxyl groups in their structure. These authors concluded that hydrolyzable tannins tend to act by directly inhibiting rumen methanogens whereas the effect of condensed tannins on CH_4 production is more through inhibition of fiber digestion. They also pointed out that more animal research is needed with these compounds to establish their antimethanogenic effect. Hydrolyzable tannins are hydrolyzed in the rumen and some could be toxic (Lowry et al., 1996; McSweeney et al., 2003).

Of the 9 studies with saponins summarized by Goel and Makkar (2012), 6 reported decreased CH_4 from about 6 to 27% (absolute production or per unit of BW or DMI). In one of these studies, however, OM digestibility was decreased, and in another 3, digestibility was not reported. From this analysis, it appeared that there was no difference in the CH_4–mitigation effect between steroidal saponins (*Yucca schidigera*) and triterpenoid saponins (*Quillaja saponaria*); *Y. schidigera* and *Q. saponaria* have been studied the most as sources of saponins because of their commercial availability. Studies from China have reported decreased CH_4 in ruminants treated with tea triterpenoid saponins but also substantial changes in microbial populations, including a reduction in protozoal counts (Wang et al., 2012).

A large number of in vitro experiments have investigated the CH_4 mitigating potential of essential oils and their active ingredients (Calsamiglia et al., 2008; Bodas et al., 2008; Benchaar et al., 2009). Unfortunately, very few have followed up the in vitro work with in vivo experiments. In most cases, these PBAC have not been successful as CH_4 mitigating agents (Beauchemin and McGinn, 2006; Benchaar et al., 2007; Van Zijderveld et al., 2011a). In their recent review on the topic, Benchaar and Greathead (2011) concluded that some essential oils (e.g., garlic

and its derivatives and cinnamon) reduce CH_4 production in vitro. These compounds, however, have not been studied extensively in vivo, and there is no evidence that they can be used successfully to inhibit rumen methanogenesis. In some cases, as with *Origanum vulgare* leaves, the in vivo effect on CH_4 mitigation was confirmed, and there was also a trend for increased feed efficiency in dairy cows (Tekippe et al., 2011; Hristov et al., 2013a), but these results need to be confirmed in long-term experiments.

Exogenous Enzymes

The use of exogenous enzymes (**EXE**) in ruminants has been intensively studied during the last 20 yr, and Grainger and Beauchemin (2011) recently reviewed their potential application to reduce CH_4 production in the rumen. There is no evidence of a direct effect of these preparations on CH_4 production, but they appear to improve diet digestibility and animal production in some studies. The responses, however, are inconsistent and the factors affecting the responses are not clearly understood. Recently, some EXE were shown to increase feed efficiency in dairy cows (by 10 to 15%; Arriola et al., 2011; Holtshausen et al., 2011) and reduce CH_4 when added to the whole diet. Improved feed digestibility might decrease fermentable OM in (stored) manure, thus reducing overall CH_4 emissions from some ruminant production systems. On the other hand, some EXE products may in fact increase CH_4 production. An EXE with endoglucanase and xylanase activities, for example, increased CH_4 production per unit of DMI or milk yield by about 10 to 11% in a study by Chung et al. (2012), but no information was provided to explain their findings.

Direct-Fed Microbials

Direct-fed microbials (**DFM**), in one form or another, are commonly used as supplements in animal production. Probably the most common DFM used in ruminant nutrition are yeast-based products (**YP**). The notion of using YP to mitigate CH_4 production has been discussed (Newbold and Rode, 2006), but with the exception of some exciting and unconfirmed in vitro results (Chaucheyras et al., 1995), convincing animal data to support this concept are lacking.

Meta-analyses reported an overall positive effect of various YP on milk yield in dairy cows (Van Vuuren, 2003; Desnoyers et al., 2009; Robinson and Erasmus, 2009; Poppy et al., 2012). The Robinson and Erasmus (2009) review reported that *Saccharomyces cerevisiae* YP increased milk yield by 3.6% on average (over the control). The same YP had no effect on feed intake or milk production and composition of high-producing dairy cows (Hristov et al., 2010b), which only emphasizes the variability and conditional effects of these products.

Other DFM interventions of ruminal fermentation include inoculation with lactate-producing and lactate-utilizing bacteria to promote more desirable intestinal microflora and stabilize pH and promote rumen health, respectively. A meta-analysis by Krehbiel et al. (2003) reported a generally positive trend for improved health in young, growing dairy or beef cattle treated with various DFM (mainly based on *Lactobacillus* and *Streptococcus* and in some cases *Propionibacterium* spp.). Several studies have reported a successful establishment of DFM products based on *Megasphaera elsdenii* (one of the most important lactate-utilizing species in the rumen) in sheep and cattle, but effects on ruminal pH and fermentation have been inconsistent (Klieve et al., 2003; Henning et al., 2010). There have also been other attempts to inoculate the rumen with fungi (*Candida kefyr*) and lactic acid bacteria (*Lactococcus lactis*) along with nitrate supplementation to both control methanogenesis and possibly prevent nitrite formation, but no consistent animal data have been reported (Takahashi, 2011). Although fermentation of lactate to VFA would help prevent a decreased ruminal pH, introduction of lactate-producing DFM would require careful scrutiny in situations in which subacute rumen acidosis might occur.

Defaunation

Association and cross-feeding between ruminal protozoa and archaea have been established (Vogels et al., 1980; Lee et al., 1987; Finlay et al., 1994) and are the basis for suggesting defaunation as a CH_4 mitigation strategy (Newbold et al., 1995; Boadi et al., 2004; Hristov and Jouany, 2005). However, the response in CH_4 production to partial or complete defaunation has been variable. Morgavi et al. (2010) calculated an average decrease in CH_4 production of about 10% due to defaunation, but the data from that study were extremely variable. Moreover, all responses were attributed to loss of protozoa without accounting for depressed ruminal fiber digestibility, which promotes acetate and/or CH_4 fermentation pathways and typically accompanies defaunation (Eugène et al., 2004). Research from the latter group with beef cattle reported no effect on rumen methanogen abundance despite a 65% difference in protozoal numbers between a high-forage and a high-starch, lipid-supplemented diet (Popova et al., 2011). Similarly, a 96% reduction in ruminal protozoa had no effect on methanogenic archaea in dairy cows treated with lauric acid (Hristov et al., 2011b).

With such variability and uncertainty in the response (see Morgavi et al., 2011), defaunation cannot be recommended as a CH_4 mitigation practice. Apart from lauric acid and coconut oil (Sutton et al., 1983; Machmüller and Kreuzer, 1999; Hristov et al., 2004, 2009, 2011b; Holl-mann and Beede, 2012), which can severely depress DMI in cattle, and some vegetable oils with a high proportion of unsaturated fatty acids (**FA**) such as linseed (Doreau and Ferlay, 1995), there has been no effective and practical defaunating agents tested comprehensively in vivo.

Manipulation of Rumen Archaea and Bacteria

Significant efforts have been devoted to suppressing archaea and/or promoting acetogenic bacteria in the rumen. Vaccines against rumen archaea are based on the concept of a continuous supply of antibodies to the rumen through saliva. Vaccines against archaea have been successful in vitro (Wedlock et al., 2010) but not in vivo (Wright et al., 2004; Williams et al., 2009). Vaccines prepared from New Zealand and Australian methanogen strains proved unsuccessful in reducing CH_4 production in ewe lambs (Clark et al., 2004).

New approaches have involved identification of genes encoding specific membrane-located proteins from *Methanobrevibacter ruminantium* (perhaps the most important rumen methanogen) and using purified proteins (produced in *Escherichia coli*) as antigens to vaccinate sheep (Buddle et al., 2011). In another approach, antisera were generated in sheep against subcellular fractions from *M. ruminantium*, which reduced microbial growth and CH_4 production in vitro (Wedlock et al., 2010). Sequencing the genome of *M. ruminantium* has opened new frontiers and opportunities for inhibition of rumen methanogens and the potential to mitigate ruminant CH_4 emissions (Leahy et al., 2010). Ruminal bacteria capable of utilizing hydrogen and CO_2 to produce acetate exist in the rumen (Joblin, 1999), and although these bacteria do not seem to be able to compete with methanogens for hydrogen under normal ruminal conditions (Fievez et al., 2001), they might be competitive if dissolved hydrogen concentrations increase as a result of suppressed CH_4 production (Le Van et al., 1998). The model of Janssen (2010) proposes a dynamic interaction between dissolved hydrogen, passage rate, propionate production, and the growth and activity of methanogens in the rumen. These interactions need to be acknowledged in the development of vaccines, and this is an exciting and fast-developing area of research that may produce effective CH_4 mitigation technologies in the future (Wright and Klieve, 2011).

Recent research has suggested that interventions in early life of the animal can trigger differential microbial rumen colonization and development, which may result in differential rumen CH_4 production. In a study by Abecia et al. (2011), kids from does treated with BCM had reduced CH_4 production compared with kids from untreated dams (although animals were group fed and individual DMI was not reported), introducing the pos-

sibility that responses to rumen modifiers may be influenced by the mother and remain programmed in the animal's adult life. This interesting concept may offer new opportunities for mitigating CH_4 emission in ruminants but needs to be further tested and verified. Another interesting approach, using antimethanogen antibodies to suppress CH_4 production, was shown to be ineffective in vitro (Cook et al., 2008).

Dietary Lipids: Vegetable Oils

There is a large body of evidence that lipids (vegetable oil or animal fat) suppress CH_4 production. The effects of lipids on rumen archaea are not isolated from their overall suppressive effect on bacteria and protozoa. Several reviews have attempted to develop prediction factors for the effect of feed lipids on CH_4. Giger-Reverdin et al. (2003) found the following relationship between CH_4 production and dietary fat [as ether extract (**EE**)]: CH_4 (L/kg DMI) = 47.3 − 0.0212 × DMI^2 (kg/d) − 0.680 × EE (%) ($R^2 = 0.76$, $n = 37$). Eugène et al. (2008) reported a 9% reduction in CH_4 production in dairy cows due to lipid supplementation of the diet, but this was accompanied by a 6% reduction in DMI, which resulted in no difference in CH_4 per unit of DMI. However, these authors also reported that lipid supplementation had no effect on 4% fat-corrected milk (**FCM**), which, combined with the reduced DMI, resulted in a trend for increased feed efficiency with oil supplementation. A more recent meta-analysis of 38 research papers reported a consistent decrease in DMI with all types of dietary fat examined (tallow, various calcium salts of FA, oilseeds, and prilled fat), but milk production was increased (Rabiee et al., 2012). This combination of decreased DMI and maintained or increased milk production (assuming no decrease in milk fat) results in increased feed efficiency and, consequently, decreased CH_4 Ei.

The greater inhibitory effect of unsaturated vs. saturated FA on rumen microbial activity reported by Palmquist and Jenkins (1980) and Nagaraja et al. (1997) does not appear to apply to CH_4 production in most studies (Beauchemin et al., 2007b; Van Zijderveld et al., 2011a; Sauvant et al., 2011) although a greater mitigating effect of polyunsaturated FA was observed in the analysis by Doreau et al. (2011). Biohydrogenation of unsaturated FA can also serve as a hydrogen sink, but it has been suggested that only 1 to 2% of the metabolic hydrogen in the rumen is used for this purpose (Czerkawski and Clapperton, 1984; Jenkins et al., 2008).

Meta-analyses by Moate et al. (2011) and Grainger and Beauchemin (2011) documented a consistent decrease in CH_4 production with fat supplementation. Moate et al. (2011) reported the following relationship between dietary fat and CH_4 production per unit of DMI:

CH_4 (g/kg DM) = 24.51 (±1.48) − 0.0788 (±0.0157) × fat (g/kg DM). Grainger and Beauchemin (2011) analyzed 27 studies and concluded that, within a practical feeding rate of less than 8% fat in the diet, a 10 g/kg increase in dietary fat would decrease CH_4 yield by 1 g/kg DMI in cattle and 2.6 g/kg in sheep. However, all of these studies either scale CH_4 per unit of DMI (i.e., disregarding the likelihood of an increased need for replacement animals if DMI and subsequent milk production are depressed) or included DMI as a variable (i.e., assuming that DMI can be maintained or predicted accurately). Prediction equations could account for these effects by substituting the response of fat on DMI into a subsequent equation relating the effect of fat on CH_4, as done for RDP's responses on DMI and milk protein production (Firkins et al., 2006).

The important question of persistence of the effect of lipids on CH_4 production has not been adequately addressed. In a study with dairy cows on pasture, Woodward et al. (2006) examined the effect of vegetable and fish oils on milk production and CH_4 emission after 14 d and again after 12 wk. Lipids significantly decreased CH_4 production in the short term, but this effect was not observed after 11 wk of feeding lipids. These authors concluded that lipids were not beneficial for milk production and emphasized the need for long-term studies when developing on-farm strategies for CH_4 mitigation with grazing animals. Grainger and Beauchemin (2011) examined 6 long-term studies (6 to 36 wk, mostly with dairy cows) and concluded that the effect of dietary fat on CH_4 production persists but the effect is not consistent among studies. Persistence of the mitigating effect of dietary oil was also observed in the study of Martin et al. (2011) with flaxseed in dairy cows although it was not supported by another study from the same group with young bulls (Eugène et al., 2011).

In some studies, lipids had a significant and negative impact on DMI (e.g., Martin et al., 2008), a factor that must be carefully considered both in prediction of mean responses and for risk assessment by those choosing to adopt these mitigation strategies. Another important factor to take into account with lipids is that mitigation of CH_4 tends to correspond with increased likelihood of depressing milk fat and/or protein concentration, potentially with enhanced responses when combining lipids with other strategies such as ionophores (Mathew et al., 2011). Some fats such as coconut oil, for example, can severely depress feed intake, fiber digestibility, and, consequently, milk production and cause milk fat depression in dairy cows (Hristov et al., 2004, 2009, 2011b; Lee et al., 2011; Hollmann and Beede, 2012) although they may be still beneficial as CH_4 mitigating agents (Machmüller and Kreuzer, 1999; Machmüller, 2006; Hristov et al., 2009). Even a blend of mostly saturated long-chain

FA (C16:0, C18:0, and C18:1) was found to cause a significant drop in feed intake and milk production and a marked decrease in milk fat percentage (from 3.10 to 2.51%; a clear indication of milk fat depression although not statistically significant; Hollmann and Beede, 2012). Lipids causing this kind of production effects cannot be recommended as mitigation agents.

Dietary Lipids: By-Products

Although supplementing animal diets with edible lipids for the sole purpose of reducing CH_4 emissions is debatable, high-oil by-products from the biofuel industries [dry (**DDG**) or wet (**WDG**) distillers grains alone or with solubles (**DDGS** and **WDGS**, respectively) and mechanically extracted oilseed meals] can naturally serve as a CH_4 mitigating feed, if included in the diet to decrease feed cost. McGinn et al. (2009), for example, reported up to 24% less CH_4 emissions when DDG replaced barley grain in the backgrounding diet of beef cattle by supplementing an additional 3% lipid to the dietary DM. However, the effects of distillers grains on CH_4 production are not consistent and might depend on the rest of the diet. Hales et al. (2013) fed diets containing 0 to 45% WDGS (substituting steam-flaked corn) to Jersey steers and observed a linear increase in CH_4 emission per unit of DMI (up to 64% increase with the highest inclusion rate), due primarily to increased NDF intake, although the EE content of the diet increased from 5.9 to 8.3%.

High-oil by-product feeds might have the same suppressive effect on feed intake as free lipids, so caution must be exercised to prevent negative effects on animal productivity or milk fat depression in lactating cows (Schingoethe et al., 2009). Hales et al. (2013), for example, reported about an 11% decrease in DMI with the highest WDGS inclusion rate compared with the control. Inclusion of 12 to 13% mechanically extracted canola or rapeseed meals with various FA compositions (replacing traditional, solvent-extracted canola meal) depressed DMI and, consequently, milk production in high-producing dairy cows (Hristov et al., 2011a). These feeds also contain higher total N (but less digestible than N from the original seeds) and P, which may present an environmental challenge due to high N and P content of manure and, consequently, greater ammonia and N_2O emissions. Spiehs and Varel (2009) reported a linear increase in urinary N and total manure P excretion with increasing WDG inclusion (0 to 60%) in the diet of beef steers. Similarly, Hales et al. (2012) reported that inclusion of 30% WDGS in the diet of feedlot cattle increased total N excretion by 18% but also increased urinary N losses by 35% whereas dietary N intake was 23% higher compared with the control (0% WDGS). Distillers grains are also inherently variable in composi-

tion (Spiehs et al., 2002) and particularly in intestinal digestibility of ruminally undegraded protein and lysine limiting production in ruminants (Boucher et al., 2009). Thus, a new trend in the bioethanol industry to partially extract oil from distillers grains will decrease the energy value of the product and is likely to also decrease the CH_4 mitigating effect discussed above.

Biodiesel by-products provide high-oil feedstuffs for livestock feeding. Biodiesel can be made from various feedstocks with relatively small capital investment. With high oil yield per hectare, canola (or rapeseed) are the preferred feedstocks for biodiesel production. Mechanically extracted canola and rapeseed meals can have very high residual oil content (up to 17%, DM basis) and might depress DMI and milk production in dairy cows (Hristov et al., 2011a). The oil in these meals has a high proportion of monounsaturated FA and can impair rumen function, if included at levels exceeding 6 to 7% total dietary fat. Another product of the biodiesel industry, glycerol, has been shown to promote CH_4 production during ruminal fermentation in vitro (Czerkawski and Breckenridge, 1972).

FEEDS AND FEEDING MANAGEMENT

There is a clear relationship between feed OM digestibility, concentrate feed or starch intake, and the pattern of ruminal fermentation. As argued by Wolin (1960), the stoichiometry of ruminal fermentation dictates that more hydrogen, and consequently CH_4, will be produced with fermentation of fiber as compared with starch (in the latter case reducing equivalents are used for propionate synthesis). In a meta-analysis, Bannink et al. (2008) predicted that the fermentation of sugars and starch shifted rumen fermentation towards production of propionate when pH in the rumen decreased. Indeed, a 72 vs. 52% concentrate diet produced a 59% increase in rumen propionate concentration and a 44% drop in Ac:Pr ratio in lactating dairy cows, accompanied by milk fat depression (3.20 vs. 4.20%, respectively; Agle et al., 2010). Sauvant et al. (2011) proposed a quadratic relationship between Y_m and Ac:Pr in ruminal fluid: $Y_m = -1.89 + (4.61 \times Ac:Pr) - (0.59 \times Ac:Pr^2)$ ($n = 23$ experiments). Therefore, because of the strong relationship between forage:concentrate and Ac:Pr, increasing inclusion of grain (or feeding forages with higher starch content, such as whole-crop cereal silages) in ruminant diets should lower CH_4 production.

Effect of Feed Intake and Inclusion of Concentrates

Feed intake is an important variable in predicting CH_4 emission. Johnson and Johnson (1995) stated that as feed intake increases, the Y_m factor decreases by about 1.6 percentage points per each level of intake

above maintenance. Similarly, a linear decrease in Y_m with increasing feed intake was reported by Sauvant and Giger-Reverdin (2009). Increasing feed intake, however, usually increases fractional passage rate and decreases digestibility (NRC, 2001), which may increase excretion of fermentable OM with manure and thus CH_4 or N_2O emissions, depending on the type of manure handling system.

A strong relationship of DMI with ruminal CH_4 production has been reported by Cottle et al. (2011), Kennedy and Charmley (2012), and others and was also derived from the dataset of studies used in the report by Hristov et al. (2013b): CH_4 (g/d) = 2.54 (SE = 4.89) + 19.14 (SE = 0.43) × DMI (kg/d) (R^2 = 0.86, $P < 0.001$; Fig. 1). This simple relationship, however, ignores diet nutrient composition, which can have a significant impact on ruminal fermentation and CH_4 production. Meta-analyses by Yan et al. (2000), Sauvant and Giger-Reverdin (2009), and more recently by Ramin and Huhtanen (2013) have proposed CH_4 prediction equations involving intake or concentration of dietary variables such as OM, NDF, ADF, nonfiber carbohydrates, EE, and level of concentrate inclusion. Ellis et al. (2010) evaluated 9 CH_4 prediction equations that are currently being used in whole farm GHG models. In their analysis, equations that attempt to represent important aspects of diet composition performed better than more generalized equations.

To investigate the relationships among dietary nutrients and CH_4 production, the authors of this document developed prediction equations and identified key animal and dietary characteristics that determine CH_4 production in cattle. Data consisted of indirect calorimetric records of lactating and nonlactating cows. Diet characteristics (fiber fractions, CP, EE, and lignin), animal information (BW and breed), GEI, and year of the study were used as possible covariates that could be selected with equal probability (for details on variables selection and statistical procedures see Moraes et al., 2013). The following equations were developed for lactating and nonlactating dairy animals [in which CH_4 is expressed on a GEI basis (Mcal/d), NDF is expressed as percent NDF in the diet (DM basis), EE is expressed as percent ether extract in the diet (DM basis), and BW is expressed in kilograms].

Lactating cows: CH_4 = 0.37 (0.37) + 0.0392 (0.0015) GEI + 0.0189 (0.0077) NDF − 0.156 (0.034) EE + 0.0014 (0.0003) BW

Nonlactating animals: CH_4 = 0.074 (0.093) + 0.0409 (0.0019) GEI + 0.0039 (0.0016) NDF − 0.0432 (0.0122) EE + 0.0014 (0.00008) BW
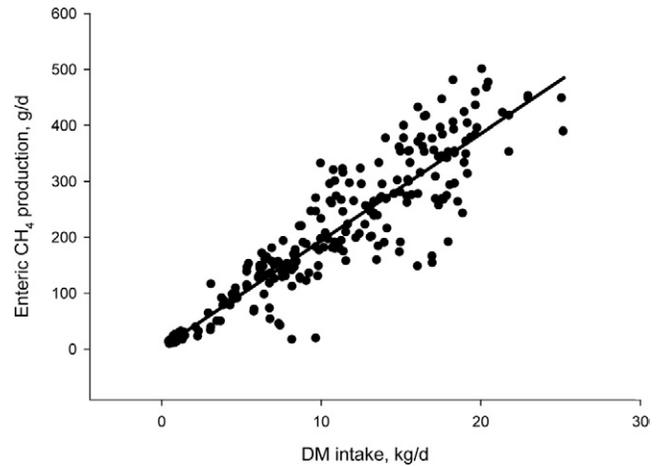

Figure 1. Relationship between dietary DM intake and enteric CH_4 (CH_4) production (from Hristov et al., 2013b): CH_4, g/d = 2.54 (SE = 4.89) + 19.14 (SE = 0.43) × DMI, kg/d (R^2 = 0.86, $P < 0.001$; n = 377).

Although equations such as the above can be useful for predicting changes in CH_4 production triggered by changes in diet ingredient or nutrient composition, they have limitations in predicting effects of mitigation strategies. Mechanistic models that describe the mechanism of CH_4 production based on knowledge of degradation processes in the rumen and type of VFA formed give better predictions than empirical models (e.g., Alemu et al., 2011) and might provide insights into possible mitigation options. Indeed, a mechanistic model is now used for GHG inventory purposes in the Netherlands as an IPCC Tier 3 alternative to the IPCC Tier 2 fixed Y_m approach to estimate CH_4 production by dairy cattle. Unlike the Tier 2 approach, the Tier 3 approach does show different behavior in CH_4 production in the past 2 decades when compared with the Tier 2 method because the mechanistic model is capable of representing changes in CH_4 production that result from changes in diet composition that occurred over these 2 decades (Bannink et al., 2011).

Importantly, dietary variables are not independent and increasing or decreasing the concentration of one entity will decrease or increase concentration of another. For example, as discussed earlier, mitigation options aimed at reducing urinary N excretion may result in elevated CH_4 emission (Dijkstra et al., 2011). Decreasing dietary concentration of CP will result in increasing concentration of other nutrients (such as starch or NDF), and these changes may affect enteric and manure CH_4 and N_2O emissions. Therefore, effects on GHG emissions as a result of changes in one nutrient have to be interpreted in the context of potential effects resulting from changes in other dietary constituents.

Increasing the proportion of concentrate in the diet will lower CH_4 emissions per unit of feed intake and animal product if production remains the same or is increased, which has been demonstrated in the classic
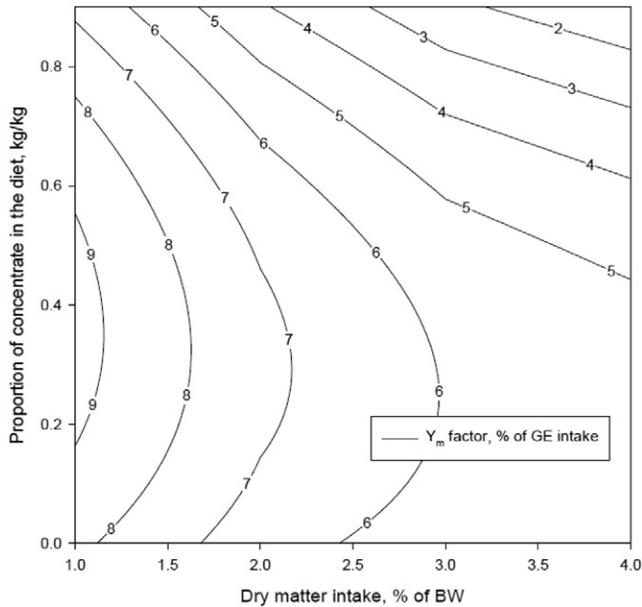
Figure 2. Effects of feed intake and proportion of concentrate in the diet on the CH_4 conversion rate factor (Y_m) (enteric CH_4 energy as percent of GE intake) (reconstructed based on the Y_m equation reported by Sauvant and Giger-Reverdin, 2009).

works of Flatt et al. (1969) and Tyrrell and Moe (1972) and reinforced by others (Ferris et al., 1999; Yan et al., 2000). Some experiments with lactating dairy cows and beef cattle have shown linear decreases in CH_4 emissions with an increase in the proportion of concentrate in the diet (Aguerre et al., 2011; McGeough et al., 2010). In a meta-analysis of 87 experiments with 260 treatments involving growing and lactating cattle, sheep, and goats, Sauvant and Giger-Reverdin (2009) concluded that marked improvements in Y_m can be expected beyond 35 to 40% inclusion of grain in the diet and this was also dependent on the level of feed intake (Fig. 2). Based on these data, small and moderate variation in dietary concentrate proportion is unlikely to affect CH_4 emission. However, concentrates generally provide more digestible nutrients (per unit feed) than roughage, which could increase animal productivity. For example, Huhtanen and Hetta (2012) in a meta-analysis of 986 dietary treatments reported a highly significant and positive relationship between dietary concentrate intake and production of milk, energy-corrected milk, and milk fat and milk protein. Hence, CH_4 expressed per unit product (i.e., Ei) is likely to decrease. Increasing the concentrate proportion in the diet above certain levels, however, might have a negative effect on fiber digestibility (Firkins, 1997; Nousiainen et al., 2009; Agle et al., 2010; Ferraretto et al., 2013), which, in addition to a potential loss of production, could result in increased concentration of fermentable OM in manure and perhaps increased CH_4 emissions from stored manure (Lee et al., 2012). Grain processing itself can have a large effect on

starch concentration in feces. Total tract digestibility of steam-flaked corn, for example, was 25% higher than that of steam-rolled corn grain in dairy cows (Firkins et al., 2001). Inclusion of steam-rolled corn (vs. stem-flaked) in beef cattle fed finishing diets (80% concentrate) resulted in extremely high starch concentrations in feces (Depenbusch et al., 2008). Thus, decreased CH_4 production (per unit of DMI) due to increased inclusion of grain in the diet may be partially offset by increased CH_4 emission from manure. To what extent these 2 processes will take place is an area that needs to be investigated and included in prediction models.

Forage Type, Quality, and Management

Forages can be categorized into fresh or conserved, with silages forming a significant portion of the latter and fed in balanced rations or as a sole diet. Silages are often fed indoors and are amenable to CH_4 measurements in respiration chambers, but fresh forages are normally grazed so intakes cannot be measured accurately in conjunction with CH_4 measurements (often with SF_6 tracer technique). Alternatively, fresh feeds can be cut and fed indoors, enabling accurate determination of intake and methane in chambers. The challenges in measuring Y_m with fresh forages are associated with imposed indoor feeding regimens and absence of selection, compared to grazing, and underestimates of Y_m measured with SF_6 from sheep fed either white clover or chicory but not ryegrass (Hammond et al., 2009, 2011; Sun et al., 2011).

An important feed characteristic that can impact CH_4 production is forage quality, specifically its digestibility. As noted by the classic work of Blaxter and Clapperton (1965), increased intake of poor-quality, less-digestible preserved forages has little effect on CH_4 production when expressed on a DMI basis (supporting the conclusion of Johnson and Johnson, 1995). For feeds with higher digestibility, however, increased DMI depresses the amount of CH_4 produced per unit of feed consumed (Hammond et al., 2009, 2013a). Moreover, it decreases CH_4 produced per unit of product by diluting maintenance energy.

The CH_4 database compiled by Hristov et al. (2013b) contained numerous references on effects of forage quality, pasture management, and processing on CH_4 production in various ruminant species. In general, CH_4 reductions are correlated with greater nutrient quality and digestibility, which are 2 attributes for which forage type and maturity might be indicators. Grazing management might be used as a potential mitigant through grazing forages at the optimal maturity for increasing forage quality, allowing for adequate pregrazing herbage mass or intensive grazing. The impact on CH_4 mitigation, when scaled per unit of animal product, should be typically greater when animals consume higher quality forage.

A meta-analysis by Archimède et al. (2011) investigated differences in CH_4 production from animals fed C3 vs. C4 grasses and warm and cold climate legumes. The database contained 22 in vivo studies with a total of 112 observations and the authors concluded that ruminants fed C4 grasses produced 17% more CH_4 (per kg of OM intake) compared with animals fed C3 grasses and 20% more than animals fed warm climate legumes. On average, C4 grasses in the database had about 16% higher NDF content than C3 grasses (64.6 vs. 55.7%, respectively), and the greater methanogenic potential of structural vs. nonstructural carbohydrates has been documented by Moe and Tyrrell (1979). Although legumes can have a CH_4 mitigation potential, problems of low persistence in pastures and the need for long establishment periods are important agronomic constraints to widespread use of legumes in a warm climate.

In contrast, Hammond et al. (2011) reported no differences in CH_4 production (23.0 g/kg DMI) measured from sheep in chambers and fed either fresh ryegrass or white clover over a range of intakes, despite a greater than 2-fold range in readily fermentable carbohydrate:NDF ratios. Sun et al. (2011) also reported similar CH_4 yields from sheep fed either fresh chicory or ryegrass (23.3 g/kg DMI), which differed widely in chemical composition. In an analysis of CH_4 emissions from sheep fed fresh ryegrass with widely varying composition, 196 records based on SF_6 and 161 from respiration chambers showed a similar CH_4 yield (as g/kg DMI) but larger SD with SF_6 (23.4 ± 5.73) than chambers (23.1 ± 2.89) and only 20% of the variation from chamber measurements was associated with the chemical composition of feed. Over 80% of the variation in CH_4 production was explained by intake (51% by SF_6) and caution is advised when interpreting methanogenesis because methodology appears to affect the results. This was even more apparent when comparing the chamber data for sheep fed either clover or chicory (above) with previous reports by Waghorn et al. (2002) who showed sheep fed white clover, chicory, *Lotus pedunculatus*, and other legumes to have much lower CH_4 yields (12 to 17 g CH_4/kg DMI) compared with sheep fed ryegrass at 21 g CH_4/kg DMI.

There do appear to be some variations in CH_4 yield from fresh forages, with Sun et al. (2012) reporting substantially lower values (g/kg DMI) from sheep fed either rape or Swedes (*Brassica napus*) compared to kale (*Brassica oleracea*), turnip (*Brassica campestris*), or ryegrass (16.4, 16.9, 19.8, 20.6, and 22.0, respectively). However, the effects of forage quality on CH_4 emissions are often contradictory (see, for example, Hart et al., 2009, and Nishida et al., 2007), with Pinares-Patiño et al. (2003) and Molano and Clark (2008) both reporting a lack of relationship between Y_m and NDF content of grasses fed to steers and sheep, respectively.

Increasing quality or digestibility of forages will increase production efficiency and this will likely result in decreased CH_4 Ei. Keady et al. (2012) recently provided a comprehensive review of the effects of silage quality on animal performance in various production systems in Ireland. These authors concluded that a 10 g/kg increase in digestible OM concentration of grass silage DM could increase 1) daily milk yield of lactating dairy cows by 0.37 kg, 2) daily carcass gain of beef cattle by 28 g/head, 3) daily carcass gain of finishing lambs by 10 g/head, 4) lamb birth weight by 0.06 kg, and 5) ewe BW postlambing by 1.45 kg. They also pointed to the critical effect of maturity on grass silage digestibility; each 1 wk delay in grass harvest reduced digestibility by 3 to 3.5 percentage points.

Keady et al. (2012) pointed out that the use of bacterial inoculants across a wide range of ensiling conditions and of formic acid under difficult ensiling conditions is expected to increase animal performance (which will reduce CH_4 Ei). Furthermore, there is indication that silage lactic acid bacteria-based inoculants may survive in the ruminal environment and perhaps positively affect fermentation by buffering rumen pH and oxygen scavenging (Weinberg et al., 2003; Hindrichsen et al., 2012). An animal trial with one of the inoculants consistently resulting in animal production responses improved N utilization, and likely increased microbial protein synthesis in the rumen compared with the untreated silage (Muck et al., 2011). Using real-time polymerase chain reaction, elevated levels of *Lactobacillus plantarum* were found in the rumens of cows consuming inoculant-treated silage (Mohammed et al., 2012).

Some studies have indicated reduced CH_4 production with corn vs. grass silages. A report by the United Kingdom Department for Environment, Food and Rural Affairs (DEFRA, 2010) indicated a 13 and 6% reduction in CH_4 per unit of DMI and per unit of milk output, respectively, when feeding a 25:75 grass silage:corn silage diet compared with a 75:25 grass silage:corn silage diet. Urinary N excretion also tended to be reduced with the higher corn silage diet. The high corn silage diet tended to increase milk yield (by about 4%, which resulted from increased feed intake) although the difference was not statistically significant. Another comparison of corn vs. grass silage reported similar results (Doreau et al., 2012).

A comprehensive overview of the various aspects of feeding corn vs. legume vs. grass silages for lactating dairy cows was recently offered by Dewhurst (2012). Based on this review, the lower fiber content and higher passage rates of legumes appeared to decrease CH_4 production compared with grasses, which was reported in earlier studies (McCaughey et al., 1999). Dewhurst (2012) also concluded that corn silage–based diets are expected to increase DMI and milk production in dairy cows; similar trends, although less conclusive, have been

reported for legume vs. grass silages. This author suggested more research is needed to elucidate the effect of various silages on CH_4 production, particularly in the case of legume silages that have the additional benefit of reducing the carbon footprint of the production system by replacing inorganic N fertilizer. The potential increase in total carbon footprint due to change in land use and increased fertilizer inputs associated with corn silage production vs. permanent pasture should be also considered (Vellinga and Hoving, 2011; Van Middelaar et al., 2012).

Corn silage inclusion in alfalfa silage–based diets for dairy cows can also improve animal production (Dhiman and Satter, 1997; Groff and Wu, 2005) and N efficiency (Wattiaux and Karg, 2004), which might lead to decreased N losses in urine and N_2O emissions from manure application. In traditional grass silage-based production systems, such as in Ireland for example, corn silage has been shown to increase performance of finishing beef cattle and lambs under a certain crop management scenario (complete cover plastic mulch system; Keady et al., 2012). Other alternative crops, such as whole crop wheat silage, have not been beneficial, but studies with silage legumes have demonstrated improvements in ADG, food conversion, and N use efficiency in lambs offered red clover, alfalfa, and kale silages compared with those offered traditional ryegrass silage (Keady et al., 2012).

Pasture management can be an important CH_4 mitigation practice. DeRamus et al. (2003) demonstrated that management-intensive grazing offered a more efficient use of grazed forage crops and more efficient conversion of forage into meat and milk, which resulted in a 22% reduction of projected CH_4 annual emissions from beef cattle. In other studies, however, stocking rate of heifers on pasture did not have an effect on CH_4 emissions (Pinares-Patiño et al., 2007).

There has been moderate interest in the so-called "high-sugar grasses" (**HSG**; grasses with elevated concentrations of water-soluble carbohydrates) as a tool for mitigating the environmental impact of livestock. A review by Parsons et al. (2011) concluded that the prospect for reducing CH_4 emissions, whether per hectare or per unit energy intake or animal product, with HSG is uncertain. A simulation effort suggested that HSG may actually increase CH_4 emissions, but this depends on the diet composition (for example, if sugars replace CP, NDF, or both), DMI, and the units chosen to express CH_4 emissions (Ellis et al., 2012b). No effect of HSG on CH_4 emissions in dairy cows was reported recently by Staerfl et al. (2012). In the United States, research with so-called *Ante Meridiem* and *Post Meridiem* hay (i.e., hay harvested in the morning or in the afternoon with low- and high-sugar contents, respectively) has demonstrated that sheep or cattle have a preference for PM hay, due to its higher sugar content (Burritt et al., 2005; Shewmaker et al., 2006).

In a Canadian study, PM hay increased milk yield of dairy cows (Brito et al., 2008). However, there was no effect on intake or milk production of dairy cattle when allocated to fresh grass in the morning or afternoon in a study by Abrahamse et al. (2009).

Feed Processing

Processing, through its effect on digestibility, energy losses, and passage rate, can be an effective CH_4 mitigation practice (although not necessarily economically infeasible; see, for example, Hironaka et al., 1996). Grain processing can be a key factor in improving feed efficiency and reducing GHG emissions from livestock operations. Thus, summarizing the corn (and sorghum) processing literature, Firkins et al. (2001) reported increased total tract starch digestibility of steam-flaked vs. steam-rolled corn grain. This improvement in digestibility resulted in an approximately 6% increase in milk yield in dairy cows at similar DMI, which would translate into improved feed efficiency. Yang et al. (2012) compared precision processing of barley (roller settings are adjusted based on the degree of kernel uniformity) vs. conventional processing (i.e., blend of light and heavy barley and rolling with one roller setting) and found improved feed intake, digestibility, and feed efficiency with precision processing. As a result of these improvements, the authors estimated that cattle fed precision-processed barley would stay in the feedlot 25 d less and save 163 kg feed per animal. The reduction of CH_4 emissions from this particular example would be significant. A recent study by Hales et al. (2012) with steers in respiration calorimetry chambers compared dry-rolled vs. steam-flaked corn and reported increased digestibility and about 17% less CH_4 emission (per unit of DMI) with the latter treatment. Per unit of DE intake, CH_4 energy was decreased by 21% (3.30 vs. 4.18%) and Y_m was decreased by about 19% (2.47 vs. 3.04%) by steam flaking. Although these effects are logical, grain processing may have a negative effect on NDF digestibility (Firkins et al., 2001).

Mixed Rations and Feeding Frequency

Very little research is available on the effect of feeding system (i.e., component or choice feeding of forage and concentrates vs. feeding of TMR) on CH_4 production. The advantages of feeding complete rations (i.e., TMR) are a more precise nutrient allocation (Coppock, 1977) and a more precise feeding of micronutrient supplements. Nocek et al. (1986) fed dairy cows forage and concentrates separately or as TMR and observed higher FCM feed efficiency with the separate feeding system due to lower feed intake. In contrast, Maekawa et al. (2002) did not report any differences in feed intake or milk production

and composition of dairy cows fed ingredients as a TMR or separately. They concluded that the latter increased the risk of acidosis because cows ate a greater proportion of concentrate than intended (overall rumen pH tended to be lower when compared with the 50% forage:50% concentrate TMR). More research is needed to determine feeding regimes that improve feed efficiency and lower CH_4 Ei.

Very few studies have investigated the effect of feeding frequency on CH_4 emissions. The reason for including this discussion in relation to CH_4 emission is that synchronization of energy and protein availability in the rumen has long been proposed as a tool for optimizing rumen function and maximizing microbial protein synthesis. Earlier studies investigated the effect of feeding frequency from the perspective of optimizing carbohydrate fermentation in the rumen. Mathers and Walters (1982), for example, fed sheep every 2 h and concluded that, even with frequent feeding, there was considerable deviation from steady state in the rate of carbohydrate fermentation in the rumen. Methane production increased rapidly, within 30 min, after feeding and then decreased until the next 2-h cycle. A series of trials in the 1980s from the laboratory of M. Kirchgessner at the University of Munchen in Germany found that frequent feeding did not improve dietary energy use but did increase CH_4 emission when concentrate was fed more often and separately from forage or with higher CP diets (Muller et al., 1980; Röhrmoser et al., 1983). In a more recent study, feeding frequency had no effect on CH_4 production in dairy cows (Crompton et al., 2010). The literature on the effect of feeding frequency on animal production is also scarce. In practical conditions, animal consume feed multiple times during a feeding cycle, even if fed once daily. As a result, feeding frequency does not appear to have an effect on feed intake. For example, feeding first lactation dairy cows once or 4 times a day had no effect on DMI or milk production (Nocek and Braund, 1985). Similarly, Dhiman et al. (2002) did not report any production advantage of feeding lactating dairy cows once or 4 times daily. In some cases, milk production of dairy cows was reduced with frequent feeding, and this was attributed by the authors to more frequent handling (Phillips and Rind, 2001). Further discussion of this topic can be found in Hristov and Jouany (2005) and Hall and Huntington (2008).

Precision Feeding and Feed Analyses

In animal nutrition, precision feeding may have different dimensions, but from a practical standpoint and farm sustainability perspective it refers to matching animal requirements with dietary nutrient supply. Accurate prediction of animal requirements and accurate feed analyses go hand-in-hand with minimizing feed waste, maximizing production, and minimizing GHG emissions per unit of animal product. Precision feeding would likely have an indirect effect on CH_4 emission through maintaining a healthy rumen and maximizing microbial protein synthesis, which is important for maximizing feed efficiency and decreasing CH_4 Ei.

Much progress in improving animal productivity and reducing CH_4 emissions from livestock, specifically Ei, in developing countries can be achieved through proper diet formulation. Garg et al. (2013) documented remarkable progress in animal performance using a program to feed balanced rations to lactating cows and buffaloes in India. Evaluation of the nutritional status of animals showed that for 71% of the animals, protein and energy intakes were higher, and for 65%, Ca and P intakes were lower than the requirements. Balancing the rations significantly improved milk yield by 2 to 14% and milk fat by 0.2 to 15%. Feed conversion efficiency, milk N efficiency, and net daily income of farmers also increased as a result of the ration balancing. Therefore, it is of paramount importance that science-based feeding systems and feed analysis are gradually introduced in developing countries with subsistence animal agriculture. This will not only have a measurable economic benefit for the farmer but will also help maximize production and feed utilization and consequently reduce GHG livestock emissions.

Accurate analysis of feed composition is a critical step in the precision feeding process. Even in developed countries with established feed analysis networks, there is still substantial variability in feed analysis among commercial laboratories (Hristov et al., 2010a; Balthrop et al., 2011) and hence the need for standardization of analytical procedures. In intensive dairy systems, daily monitoring of forage, particularly silage DM, can have a profound effect on precision feeding of the cow for maximum production and profitability. Feed analysis technologies, such as near-infrared reflectance spectroscopy (**NIRS**), have been developing rapidly since the late 1980s and has been used routinely for quality and component analysis of grain, oilseeds, and forages for the past 2 decades. The speed and low cost of NIRS analysis makes it feasible for producers to buy ingredients based on quality and to formulate rations accurately to meet the nutrient requirements of the animals to minimize over- or underfeeding.

CONCLUSIONS

There are a number of potentially effective CH_4 mitigation practices available for the livestock sector today. Conclusions for most of the mitigating agents, feed supplements, or feeding practices discussed in this review are summarized in Table 1.

Some CH_4 inhibitors, such as BCM, although effective, cannot be recommended for this purpose because of their toxicity or ozone-depleting effect. With other compounds, such as 3NP, more data are needed before any conclusions can be made. For most compounds in this category, there are insufficient long-term in vivo data. Nitrates may be promising CH_4 mitigation agents, particularly in low-protein diets that may benefit from NPN supplementation. When nitrates are used, it is critically important that the animals are properly adapted to avoid nitrite toxicity. More in vivo studies are needed to fully understand the impact of nitrate supplementation on whole-farm GHG emissions (animal, manure storage, and manure-amended soil), animal production, and animal health. Fumaric and malic acids may reduce CH_4 production when applied in large quantities, but most results indicate no mitigating effect. The long-term effects of these compounds have not been established and costs are likely to prohibit their adoption. Ionophores, through their effect on feed efficiency and reduction in CH_4 per unit of feed, would likely have a moderate CH_4 mitigating effect in ruminants fed high-grain or mixed grain–forage diets. The effect is dose, feed intake, and diet composition dependent and is less consistent in ruminants fed pasture.

Hydrolyzable and condensed tannins may offer an opportunity to reduce CH_4 production although intake and animal production may be compromised in some, but not all, instances. The agronomic characteristics of tanniferous forages as well as the concentration and structure of the condensed tannins must be considered when they are discussed as a GHG mitigation option. Based on limited research, tea saponins seem to have CH_4 mitigating potential, but more and long-term studies are required before they can be recommended. Most essential oils or their active ingredients do not reduce CH_4 production and, when CH_4 production was reduced in vivo, the long-term effect was not established. Limited data indicate EXE may increase feed efficiency and thus indirectly reduce CH_4 production; however, inconsistencies in the data question EXE as an effective mitigation practice. There is insufficient evidence of the direct CH_4 mitigating effect of yeast and other DFM. However, yeasts appear to stabilize pH and promote rumen function, especially in dairy cattle, resulting in small but relatively consistent responses in animal productivity and feed efficiency and possible decrease in CH_4 Ei.

Defaunation of the rumen cannot be recommended as a CH_4 mitigation practice. At this point, none of the existing rumen microbial manipulation technologies are ready for practical application, but vaccines could be applied to all ruminants, including those with limited human contact, such as sheep and beef animals on pasture. It is important to appreciate that vaccines require the host to produce antibodies against some of their micro-biome that are part of a symbiotic relationship, enabling ruminant survival on fiber-based diets. To be effective, the vaccines have to cover the entire methanogen community and not just some individual taxa because of likely succession of the insensitive populations that can occupy the same (their only) niche. The extent of reductions in methanogenesis may only be 5 to 10%, and persistence of the effect is unknown, but the potential for widespread application makes this an exciting opportunity for future mitigation of CH_4 emissions.

Based on the existing data, it can be concluded that inclusion of lipids in ruminant diets will likely mitigate CH_4 production, but it may also depress feed intake and, consequently, animal productivity. Therefore, at least part of the mitigation effect reported with lipids is a result of decreased intake of dietary carbohydrate, which is a consequence of decreased DMI as a result of lipids replacing carbohydrate in the diet. The feasibility of using lipids to mitigate the environmental impact of animal production depends on its economic benefits to the producer and potential effects on feed intake (negative), productivity (negative), milk fat content in lactating animals (positive or negative), and ease of supplementation (i.e., grazing systems). High-oil by-product feeds such as distillers grains and meals from the biodiesel industry can serve as cost-effective sources of lipids with potential CH_4 suppressing effect. However, their mitigating potential has not been well established and in some cases CH_4 production may increase due to increased fiber intake. A large number of nontraditional oilseeds are being investigated as biofuel feedstocks that, if available, may be used as livestock feed and have a beneficial effect on animal productivity (through improvements in energy and protein supply), including a CH_4–mitigating effect, although data to support this concept are lacking (see Hristov et al., 2013b).

Inclusion of concentrate feeds in the diet of ruminants will likely decrease CH_4 Ei, particularly when inclusion is above 35 to 40% of DMI, but the effect will depend on basal forage quality, inclusion level, production response, effects on fiber digestibility, rumen function, milk fat content, plane of nutrition, type of grain, and grain processing. Supplementation with small amounts of concentrate feeds (to all-forage diets) will likely increase animal productivity and thus decrease overall GHG Ei although absolute CH_4 emissions might not be reduced. In spite of these potential gains, concentrate supplementation cannot be a feasible substitution for ruminants fed high-quality forages. In addition, in many parts of the world, this may not be an economically feasible and socially acceptable mitigation option. Several comprehensive meta-analyses have produced equations based on animal characteristics, feed intake, and diet composition that may be useful in predicting the effect of concentrate feed supplementation on CH_4 emissions from dairy cattle.

Increased forage digestibility is expected to increase animal production and decrease CH_4 Ei. It appears C4 grasses produce greater amount of CH_4 than C3 grasses and that introduction of legumes in warm climates may offer a mitigation opportunity although low persistence and a need for long establishment periods are important agronomic constraints. Methane emission may be reduced when corn silage replaces grass silage in the diet. Legume silages may also have an advantage over grass silage due to their lower fiber content and the additional benefit of replacing inorganic N fertilizer. With all silages, effective preservation will improve silage quality and reduce GHG Ei. Forage with higher sugar content (HSG or harvested in the afternoon) may reduce urinary N losses and, consequently, N_2O emission from manure applied to soil although more research is needed to support this concept. The best mitigation option in this category is to increase forage digestibility to improve intake and animal productivity, thus reducing overall GHG emissions from rumen fermentation or stored manure per unit of animal product.

Processing of grain to increase its digestibility is likely to reduce CH_4 production per unit of animal product. Caution should be exercised that this does not result in decreased fiber digestibility or excessively fast passage rates; therefore, some processing is recommended so the grain energy is better utilized for animal production. This mitigation practice may not be economically feasible in low-input production systems. There is little evidence of beneficial effects of synchronizing energy and protein delivery or frequency of feeding on ruminal fermentation and specifically CH_4 production. Feeding of TMR may have some advantages over component feeding in stabilizing ruminal fermentation and DMI. Closely matching animal requirements and dietary nutrient supply in all animal production systems and adoption of science-based feeding systems in developing countries with subsistence animal agriculture will help maximize production and feed utilization and consequently reduce CH_4 Ei.

Overall, increasing forage digestibility and digestible forage intake typically decreases CH_4 Ei. Other effective CH_4 mitigation practices include lipid and concentrate feeds supplementation of the diet, feed processing, and certain feed additives such as nitrates, ionophores, tannins, and perhaps some DFM. The long-term effects of many of these mitigation practices, however, have not been well established. Some additives are toxic or may not be economically feasible to implement. The conclusion of this review is that improving forage quality, optimizing rumen function for higher microbial protein synthesis through feeding of a balanced diet matching the physiological stage of the animal, and enhancing the overall efficiency of dietary nutrient use are the most efficient way of decreasing CH_4 emissions per unit of animal product.

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