Invited review: Enteric methane in dairy cattle production: Quantifying the opportunities and impact of reducing emissions

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ABSTRACT

Many opportunities exist to reduce enteric methane (CH_4) and other greenhouse gas (GHG) emissions per unit of product from ruminant livestock. Research over the past century in genetics, animal health, microbiology, nutrition, and physiology has led to improvements in dairy production where intensively managed farms have GHG emissions as low as 1 kg of CO_2 equivalents (CO_2e)/kg of energy-corrected milk (ECM), compared with >7 kg of CO_2e/kg of ECM in extensive systems. The objectives of this review are to evaluate options that have been demonstrated to mitigate enteric CH_4 emissions per unit of ECM (CH_4/ECM) from dairy cattle on a quantitative basis and in a sustained manner and to integrate approaches in genetics, feeding and nutrition, physiology, and health to emphasize why herd productivity, not individual animal productivity, is important to environmental sustainability. A nutrition model based on carbohydrate digestion was used to evaluate the effect of feeding and nutrition strategies on CH_4/ECM, and a meta-analysis was conducted to quantify the effects of lipid supplementation on CH_4/ECM. A second model combining herd structure dynamics and production level was used to estimate the effect of genetic and management strategies that increase milk yield and reduce culling on CH_4/ECM. Some of these approaches discussed require further research, but many could be implemented now. Past efforts in CH_4 mitigation have largely focused on identifying and evaluating CH_4 mitigation approaches based on nutrition, feeding, and modifications of rumen function. Nutrition and feeding approaches may be able to reduce CH_4/ECM by 2.5 to 15%, whereas rumen modifiers have had very little success in terms of sustained CH_4 reductions without compromising milk production. More significant reductions of 15 to 30% CH_4/ECM can be achieved by combinations of genetic and management approaches, including improvements in heat abatement, disease and fertility management, performance-enhancing technologies, and facility design to increase feed efficiency and life-time productivity of individual animals and herds. Many of the approaches discussed are only partially additive, and all approaches to reducing enteric CH_4 emissions should consider the economic impacts on farm profitability and the relationships between enteric CH_4 and other GHG.

Key words: enteric methane, methanogen, feed efficiency, lifetime productivity, mitigation

INTRODUCTION

Methane and Greenhouse Gas Emissions

Methane (CH_4), carbon dioxide (CO_2), nitrous oxide (N_2O), and halocarbons are greenhouse gases (**GHG**) that enhance the effects of solar and thermal radiation on surface and atmospheric temperatures and are often expressed on a CO_2-equivalent (**CO_2e**) basis. Often, different and confusing bases are used in expressing the proportions of GHG and CH_4 emissions from livestock agriculture (Lassey, 2008). Although enteric CH_4 generated in the gastrointestinal tract of livestock is the single largest source of anthropogenic CH_4 (Figure 1a), it is a lesser proportion of anthropogenic GHG emissions (Figure 1b). Methane has several natural sources (termites, wetlands, peat bogs, ocean sediments, and wildlife) and man-made sources (natural gas production, coal mining, wastewater treatment, landfills, and agriculture; Figure 1a; Lassey, 2008). Anthropogenic sources account for approximately 58% of total global CH_4 emissions (Figure 1a; EPA, 2010, 2011a).

In "Livestock's Long Shadow," the Food and Agriculture Organization of the United Nations (Steinfeld et al., 2006) stated that global livestock agriculture was responsible for 18% of the anthropogenic GHG emissions annually. Since then, several groups have rebutted that report and provided reduced estimates of the impact of
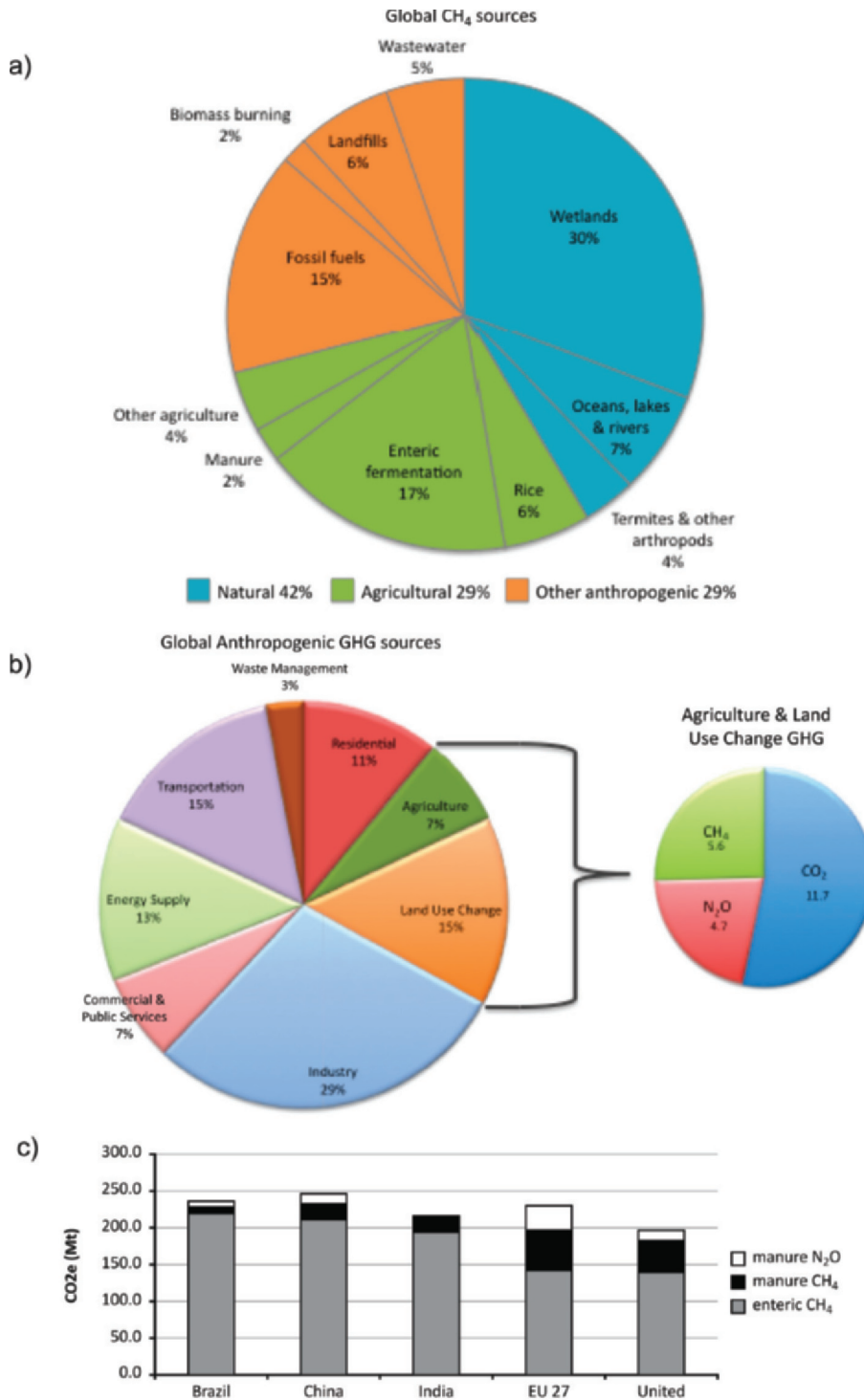
Figure 1. (a) Estimated proportion of global CH_4 emissions from natural and anthropogenic sources. Sources comprising 1% or less are not shown and include wild animals, wildfires, permafrost, and anthropogenic stationary and mobile sources. More uncertainty exists in estimates of CH_4 emissions from natural than from anthropogenic sources [data from EPA (2010) and EPA (2011a)]. (b) Global greenhouse gas (GHG) anthropogenic emissions by sector, with CH_4 and N_2O on a CO_2-equivalent (CO_2e) basis. Agriculture combined with land use change accounts for 22% of global greenhouse gas emissions. Deforestation accounts for 10.3% and fossil fuel utilization accounts for 1.4% of CO_2 released; biogenic CO_2 is not included [data from analysis by Ecofys (2013)]. (c) The 5 countries and regions with the largest livestock-associated enteric CH_4 emissions on a million-metric-tonne (Mt)-of-CO_2e basis. In the United States, 95% of enteric CH_4 arises from ruminant livestock (EPA, 2011b); this proportion can be assumed for other countries, although the contributions from beef versus dairy operations will vary. Manure CH_4 is emitted by storage systems where anaerobic fermentation occurs. Manure CH_4 and N_2O can be from either ruminant or nonruminant livestock operations [data source: EPA (2011a)]. EU 27 = European Union countries.

livestock agriculture on GHG emissions (Pitesky et al., 2009; EPA, 2011a; Petherick, 2012). Land use change (for example, converting forest or permanent pasture to annual crops) contributes a significant portion and, when combined with existing agriculture, accounts for 14 to 22% of global anthropogenic GHG emissions (Figure 1b; Shafer et al., 2011; Ecofys, 2013), although some analyses attribute little land use change to dairy production (Gerber et al., 2013; Golub et al., 2013). Approximately 37% of global agricultural CH_4 and N_2O arise from direct animal and manure emissions, and the remainder is associated with cropping and deforestation (EPA, 2011a). On a world-wide basis, dairy animals, including cull cows and beef cattle from dairy breeds, are estimated to contribute only 4% to anthropogenic GHG emissions (FAO, 2010). In many developed countries, the contribution of dairy production to GHG emissions is estimated even lower, due to the higher productivity of livestock agriculture, the dilution by emissions from other sectors, and lack of significant land use change (Hagemann et al., 2011). In the European Union 15, beef and dairy cattle are estimated to contribute 2.1 and 1.2%, respectively (EEA, 2011), to anthropogenic GHG inventories, and in the United States, all livestock (including nonruminants) and dairy cattle are estimated to contribute 2.75 and 0.55%, respectively, to anthropogenic GHG emissions (EPA, 2011b). However, in developed countries where pastoral agriculture is a significant portion of the economy (e.g., Ireland and New Zealand) or developing countries with large cattle populations (e.g., Brazil and India), ruminant livestock can be a very large contributor to the national GHG inventory (FAO, 2010).

Examining CH_4 emissions from livestock agriculture as a proportion of total anthropogenic GHG emissions in a given country or region can be misleading. Methane emissions are a function of the population of ruminant animals, their level of production, and the associated manure-handling systems. Thus, the countries or regions with the largest cattle populations in the world contribute the most to global agricultural CH_4 emissions on a million-metric-tonne basis (metric tonnes of CO_2e; Figure 1c). Why should the dairy industry in any country be concerned about CH_4 emissions? First, international policy discussions have focused on non-CO_2 emissions such as CH_4 and N_2O because they are less expensive to mitigate than CO_2 emissions (EPA, 2006; FAO, 2010; Shafer et al., 2011; Gerber et al., 2013). Often, CH_4 mitigation approaches can be economically advantageous as well as environmentally beneficial. Second, because the CO_2 emitted by livestock, including dairy cattle, arises from metabolism of plant-derived feedstuffs, it is viewed as part of a continuous biological cycle of fixation, uti-

lization, and exhalation. Accordingly, it is defined as biogenic CO_2 and livestock are considered to be a zero net source of CO_2 (Pitesky et al., 2009). Third, enteric and manure CH_4 comprise more than 40% of the GHG emissions associated with fluid milk production in the United States (Thoma et al., 2013). Last, some retailers and consumers in both domestic and international markets are concerned about the contribution of GHG emissions to the carbon footprint of foods. Ruminant livestock will play a crucial role in future global food security because far more grazing land exists, unusable for human food, than cropping land (Gill et al., 2010) and ruminant animals can transform pasture into high-quality human food. Ruminants also are very capable of converting the human-inedible by-products of food production into high-quality human food. If mitigation strategies are implemented that reduce GHG but also reduce production output, then the environmental benefits would be at least partly negated by increased food costs or reduced supply of animal-based foods.

Enteric CH_4 comprises 17 and 3.3% of global CH_4 and GHG emissions, respectively, and is largely derived from ruminant livestock (Figures 1a and 1b). Manure CH_4 from both ruminant and nonruminant livestock contributes 2 and 0.4% of global CH_4 and GHG emissions, respectively (Figures 1a and 1b). Several country and regional GHG inventories do not differentiate between ruminant and nonruminant livestock production systems with regard to manure GHG emissions. Manure CH_4 emissions are a larger proportion of total farm CH_4 emissions in intensively managed dairy operations with manure storage systems, and much lower in extensive or grazing operations (Figure 1c). Manure N_2O emissions contribute <1% of global GHG emissions (Ecofys, 2013). Significant interrelationships exist between enteric CH_4 and manure CH_4 and N_2O emissions, and accordingly, mitigation approaches targeted at reducing enteric CH_4 must consider the effect on manure CH_4 and N_2O emissions. Because of the larger contribution of enteric CH_4 than manure CH_4 and N_2O in dairy production to agricultural GHG emissions, this review focuses on enteric CH_4. Readers are referred to Gerber et al. (2013) and Hristov et al. (2013) for an integrated discussion of enteric and manure GHG emissions and mitigation opportunities from ruminant livestock.

This review will provide a broad, integrated view of CH_4 mitigation opportunities in dairy production for agricultural students and scientists. The objectives are to (1) evaluate options that have been demonstrated to mitigate enteric CH_4 emissions from dairy cattle on a quantitative basis and in a sustained manner; (2) integrate approaches in genetics, feeding and nutrition, physiology, and health to emphasize why herd productivity, not individual animal productivity, is

important to environmental sustainability; and (3) provide perspective on the relative contribution of enteric CH_4 emissions from dairy production to global GHG emissions. The majority of the research presented was conducted under intensive management conditions in temperate climates. In principle, the approaches discussed can be applied to any dairy production system because their aim is increasing productivity at the herd level. Enteric CH_4 per unit of ECM (g of CH_4/ kg of ECM) will be the evaluation basis for 2 reasons. First, dairy farmers will not be willing to implement CH_4 mitigation strategies if they decrease milk production, for which farmers are not compensated. Second, as the world population continues to grow during this century, agriculture must focus on production efficiency to provide an adequate food supply, and milk and dairy foods are an important source of calories as well as protein and micronutrients. Thus, enteric CH_4 emissions per unit of ECM (CH_4/ECM) is the correct and most useful basis biologically, nutritionally, environmentally, and economically. Some of the mitigation approaches can be readily implemented at this time, and others need short-term development (2 to 5 yr). In vitro studies are presented where appropriate, but the focus of this article is in vivo research. Although in vitro studies are a valuable way to test ideas, in vivo experiments are imperative for obtaining quantitative results that capture the complexity and dynamics of ruminant digestion and metabolism and the consequences on lactation performance.
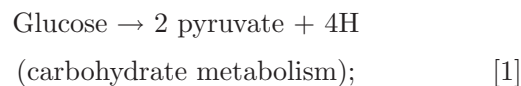
To identify effective mitigation strategies, accurate and repeatable measurement techniques are required. Several direct and indirect methods have been used to quantify CH_4 emissions in vivo, many of which were reviewed by Johnson and Johnson (1995), Kebreab et al. (2006), and Storm et al. (2012), including their advantages, disadvantages, and limitations. The most common in vivo measurement techniques are respiration calorimetry (either closed or open-circuit), polyethylene tunnel system, isotope dilution, tracer gas [i.e., sulfur hexafluoride (SF_6)], and micrometeorological mass balance (Kebreab et al., 2006). New technologies are also being developed to assess CH_4 concentrations on an hourly basis using rumen sensors (Laporte-Uribe and Gibbs, 2009) or in commercial operations by measuring CH_4 eructated during eating in robotic milking stations or at pasture feeders (Utsumi et al., 2011). Comparisons of the measurement techniques have identified systematic differences (Kebreab et al., 2006; Muñoz et al., 2012). Respiration chambers remain the gold standard in research settings that permit animal confinement. Improvement of the other existing methodologies or development of new methodologies that allow for repeatable, accurate CH_4 emission measurements from groups of animals or in different housing situations is critical in evaluating mitigation strategies.

Rumen Function: Ecology and Biochemistry

Ruminant animals and microbes have evolved together, filling a niche based on the conversion of complex plant carbohydrates to energy that is beneficial to both the host animal and the microbial symbionts. The microbes include bacteria, protozoa, fungi, and Archaea (Figure 2). The rumen ecosystem is an anaerobic environment, in which the degradation of plant material occurs in a very short time frame compared with other anaerobic ecosystems such as wetlands and estuaries, and the fermentation products are different. Some of the microbial species have coevolved with ruminants and hindgut-fermenting mammals and do not exist in any other environment (e.g., rumen protozoa). Also, the methanogens of ruminants and other mammalian herbivores are distinct from methanogens in other environments. To date, 3 major genera and 3 minor genera of methanogens belonging to the Archaea domain have been identified, although it is likely that more exist (Wright et al., 2006; Janssen and Kirs, 2008; Liu and Whitman, 2008; Kong et al., 2013; Poulsen et al., 2013). Only 8 methanogen species have been cultured (Kong et al., 2013) and the total number of rumen archaeal species is unknown (Janssen and Kirs, 2008), but has been estimated to be approximately 360 to 1,000 on an operational taxonomic unit basis (Kim et al., 2011; Kong et al., 2013). Methanogens are found in the hindgut as well as the rumen, although the population structure, ecology, and microbial metabolism differ between the 2 compartments.

In the reticulorumen and hindgut, simple and complex carbohydrates are hydrolyzed to 5- and 6-carbon sugars by microbial enzyme activity. Sugars are fermented to VFA through multiple-step pathways that produce reducing equivalents (i.e., metabolic hydrogen), which can be summarized in the following equations (Hungate, 1966; Czerkawski, 1986; Moss et al., 2000):

$$\text{Glucose} \rightarrow 2 \text{ pyruvate} + 4\text{H}$$
$$\text{(carbohydrate metabolism);} \qquad [1]$$

$$\text{Pyruvate} + \text{H}_2\text{O} \rightarrow \text{acetate} + \text{CO}_2 + 2\text{H}; \qquad [2]$$

$$\text{Pyruvate} + 4\text{H} \rightarrow \text{propionate} + \text{H}_2\text{O}; \qquad [3]$$

$$2 \text{ acetate} + 4\text{H} \rightarrow \text{butyrate} + 2\text{H}_2\text{O}. \qquad [4]$$

The metabolic hydrogen is converted to H_2 by hydrogenase-expressing bacterial species, and the H_2 converted to CH_4 by Archaea in the combined reaction:

$$CO_2 + 8H \rightarrow CH_4 + 2H_2O \text{ (methanogenesis).} \quad [5]$$

Dissolved H_2 inhibits ruminal fermentation pathways through negative feedback mechanisms, and if not removed by the methanogens, will reduce the overall extent of carbohydrate degradation, the rate of microbial growth, and the synthesis of microbial protein (Wolin, 1974; McAllister and Newbold, 2008). Biohydrogenation of FA provides an alternative hydrogen sink to methanogenesis (Figure 2). Degradation of dietary protein and assimilation into microbial protein can result in either a net consumption or net production of hydrogen (Figure 2; Hungate, 1966; Czerkawski, 1986). Additionally, previously unknown methanogens of the order Thermoplasmatales that use methyl groups rather than H_2 have been recently identified in the rumen (Poulsen et al., 2013). This group and other unidentified organisms may help explain the lack of predictability in the effects of various rumen manipulations that has been observed in the past.

As a consequence of the complex H_2 and methyl group metabolism in the reticulorumen, changes in pathways leading to VFA production, biohydrogenation, microbial N metabolism, and microbial growth will alter the amount of CH_4 produced (Figure 2). These changes are dynamic functions of both microbial populations (species, abundance, and activity of microbes) and which pathways are being utilized, which contributes to the complexity and difficulty of predicting CH_4 emissions and developing mitigation strategies.

METHANE MITIGATION STRATEGIES

An abundance of CH_4 mitigation strategies have been studied and they can be classified into 3 broad categories:

1. Feeds, feeding management, and nutrition: feeding good-quality feeds can increase animal productivity and feed efficiency. Certain feeds can enhance propionate or decrease acetate production (Equations 2 and 3), decreasing H_2 that would be converted to CH_4.
2. Rumen modifiers: feeding specific substances that directly or indirectly inhibit methanogenesis or using biological control (defaunation, bacteriocins, bacteriophages, and immunization) directed at reducing methanogens.
3. Increasing animal production through genetics and other management approaches: improving nutrient utilization for productive purposes to dilute out maintenance on an individual animal or a herd basis, increasing feed efficiency and decreasing CH_4 per unit of product (meat or milk).
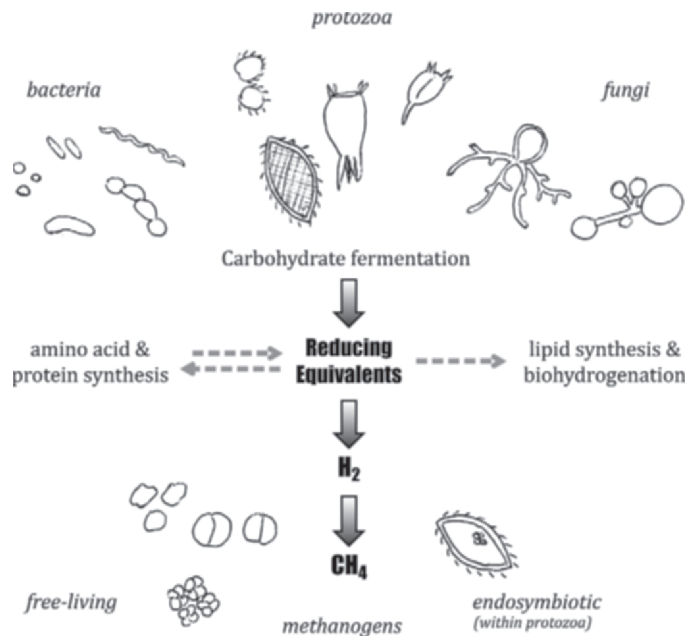
Figure 2. Rumen microorganisms, including bacteria, protozoa, and fungi, ferment carbohydrates to obtain energy and generate significant amounts of reducing equivalents ($FADH_2$, NADH, and others) in the process and VFA (not shown) and H_2 as end products. Methanogens, both free living and endosymbionts inside protozoa, convert H_2 to CH_4. A small amount of reducing equivalents are utilized in lipid synthesis and FA biohydrogenation. Synthesis of amino acids can result in production or utilization of reducing equivalents, but the net amount is small. Protein synthesis utilizes reducing equivalents. Elevated concentrations of H_2 inhibit carbohydrate fermentation, providing a negative feedback mechanism. Organisms are not drawn to scale [after Czerkawski (1986)].

Total CH_4 emissions will be decreased if annual production of milk remains constant and fewer cows are needed to produce the same amount of milk.

Although dairy cows are of primary concern, studies using other ruminant animals (sheep, goats, or beef cattle) are included as appropriate for reference. Many of the principles behind CH_4 reduction can be generalized to include all ruminants. However, the right mitigation approach must be adapted to the specific needs of the farmers and animals. Although the majority of the CH_4 mitigation approaches discussed were studied with animals in confinement housing and fed feeds grown in temperate climates, with appropriate consideration of the underlying biology, their application can be extended to other production systems. Most importantly, mitigation strategies should be cost effective or cost neutral if we expect farmers to adopt the changes.

Feeds, Feeding Management, and Nutrition

Nutritional mitigation of CH_4 production is founded on 3 basic approaches: (1) ingredient selection to alter

VFA production patterns; (2) increased rate of passage, which can alter microbial populations and VFA production patterns and shift some digestion to the intestines; and (3) feeding better-quality diets to increase milk production per cow, which will dilute the CH_4 cost associated with maintenance energy requirements.

Feed ingredients provide the substrates for microbial fermentation, and differences in feed digestibility and chemical composition alter the amount of energy extracted by the microbes and the patterns of VFA and CH_4 produced. The proportions of VFA affect the amount of CH_4 produced, because propionate formation consumes reducing equivalents, whereas acetate and butyrate formation generate H_2 for methanogenesis (Hungate, 1966). As such, any dietary component or intervention that causes a shift in favor of propionate production will be accompanied by a reduction in CH_4 production per unit of feed fermented, whereas the opposite is true for acetate and butyrate (Van Nevel and Demeyer, 1996). Rumen protein degradation and assimilation into microbial protein can result in either a net consumption or net production of H_2 (Figure 2; Hungate, 1966; Czerkawski, 1986). Biohydrogenation of FA will result in a net consumption of H_2 (Figure 2). Consequently, variations in rumen N metabolism and biohydrogenation will cause alterations in CH_4 production, and because carbohydrate and protein substrates are also used for microbial maintenance and growth, theoretical predictions of VFA patterns and CH_4 formation do not always correlate to in vitro and in vivo observations (Hironaka et al., 1996).

Passage rate also affects the extent of digestion and patterns of VFA formation as well as microbial growth rates and has been found to explain 28% of the variation in CH_4 emissions (Okine et al., 1989). Faster passage of feed material out of the rumen means a lower extent of rumen fermentation and possibly less CH_4 production per unit of feed, depending on whether the feed nutrients are digested in the small intestine (sugars and starches) or fermented in the hindgut (pectin, glucans, and NDF). Increased passage rates also increase microbial energy requirements because cells have to divide more frequently to maintain rumen populations.

High-quality (more energy-dense or more digestible) diets provide more energy for production as a proportion of the gross energy intake (**GEI**) and dilute the costs of maintenance than low-quality diets; therefore less CH_4/ECM is generated (Figure 3). More energy-dense diets usually contain higher proportions of starch relative to NDF, and less CH_4 is produced per unit of starch digested than NDF (Moe and Tyrrell, 1979). These diets also can increase net energy intake and if the net energy is partitioned to milk, it will decrease CH_4/ECM production. However, reducing enteric CH_4 has a small effect on animal energetics. For a cow producing 30 kg of ECM and 450 g of CH_4 per day, a 15% reduction in CH_4/ECM would provide an additional 0.9 Mcal/d to an estimated ME intake of 53 to 57 Mcal/d, assuming that digestibility is not affected.

These alterations in digestibility, proportions of VFA produced, and microbial growth affect energy and protein availability to the cow and, ultimately, the efficiency at which the feed nutrients are used for productive functions, including growth and milk synthesis (NRC, 2001). Based on these 3 principles, CH_4 emissions can be affected by the level of feed intake, type of carbohydrate, forage quality and species, physical processing, forage preservation, and feeding frequency (Table 1).

Level of Intake, Digestibility, and Passage. Many studies have found that variation in DMI accounts for 52 to 64% of the variation in CH_4 production on a per day basis when cattle were fed ad libitum (Boadi and Wittenberg, 2002; Pinares-Patiño et al., 2007; Hammond et al., 2009). To account for the effects of DMI on digestibility, a static model was developed based on reductions in starch digestibility (Firkins et al., 2001) and NDF digestibility (Huhtanen et al., 2009) with increasing DMI and using CH_4 prediction equations based on digestible carbohydrate fractions (Moe and Tyrrell, 1979). Dry matter intake was predicted from milk yield and composition using the dairy NRC (2001) model, and results for a 680-kg lactating cow consuming a ration with 50% forage, 30% NDF, and 25% starch are shown in Figure 3. Total CH_4 production (g or Mcal/d) increases with increasing DMI because there is more feed to be fermented (Figure 3a). However, CH_4 as a proportion of DMI or GEI (g of CH_4/kg of GEI) usually decreases as DMI increases above maintenance (Blaxter and Clapperton, 1965; Moe and Tyrrell, 1979; Pinares-Patiño et al., 2009) and is related to decreases in DM digestibilities observed at higher intakes and the associated increases in passage rates (Figure 3b). The relationship between CH_4 emitted (kg/d or Mcal/d) and DMI or GEI is not constant, but decreases as intake increases. Accordingly, CH_4/ECM decreases with increasing DMI and milk yield (Figure 3a). For example, a cow producing 30 kg of milk/d and consuming a 50% forage and 50% concentrate ration is predicted to emit 12.7 g of CH_4/kg of ECM compared with a cow producing 35 kg of milk/d with the same diet, emitting 11.9 g of CH_4/kg of ECM.

Whereas digestibility was estimated to decrease 4.6% per multiple of maintenance in the older literature (Tyrell and Moe, 1975), under current feeding situations with better-quality forages and improved feeding management, digestibility depression is probably <2 or 3% per multiple of maintenance (Vandehaar, 1998; Sauvant and Giger-Reverdin, 2009). Also, it is possible
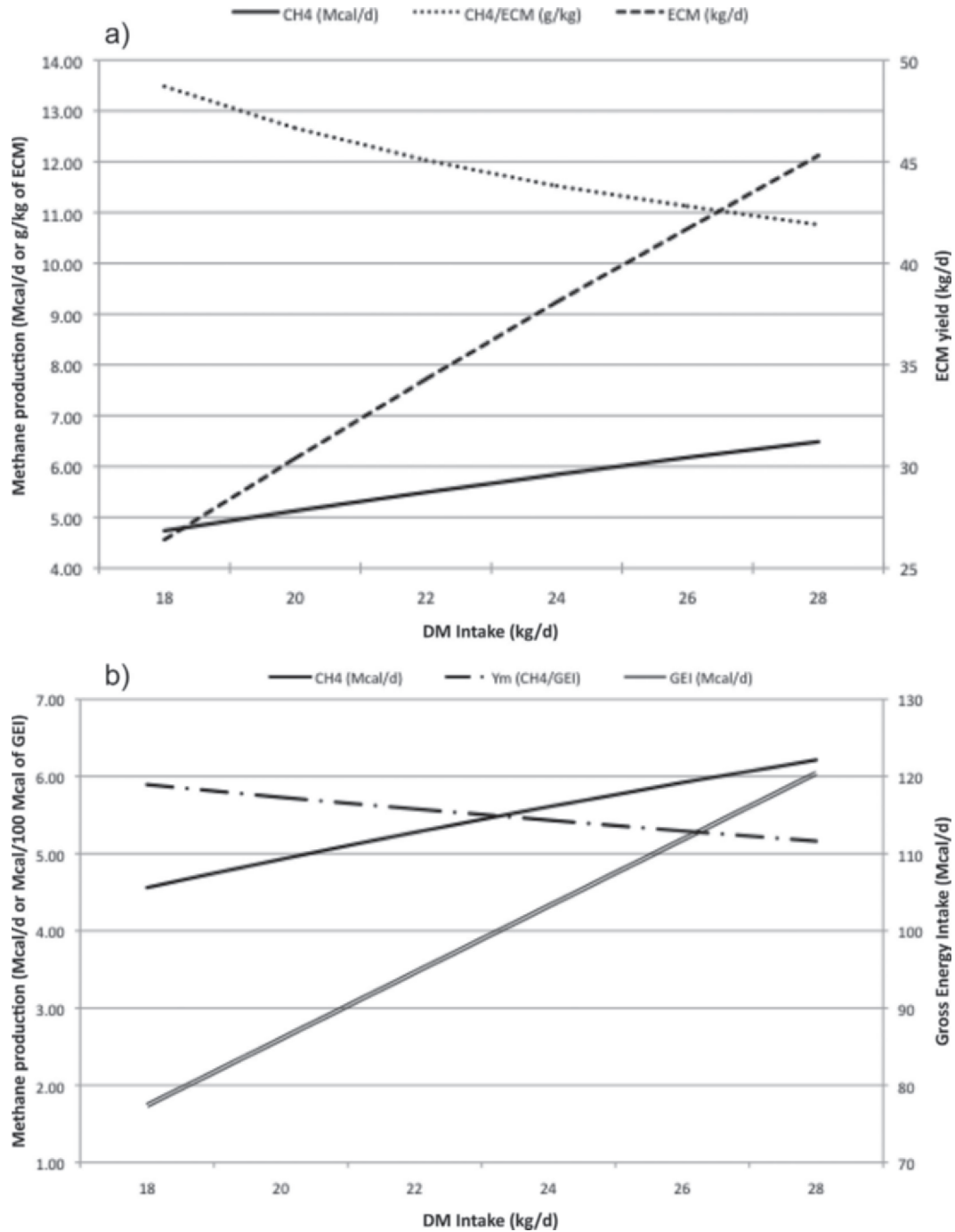
Figure 3. (a) Energy-corrected milk yield (dashed line) increases more rapidly than CH_4 production (solid line) with increasing DMI, resulting in less enteric CH_4 emissions per unit of ECM (CH_4/ECM; dotted line). (b) Corresponding decreases in CH_4 as a proportion of gross energy intake [GEI; g of CH_4/kg of GEI (Ym; CH_4/GEI); dashed + dotted line] are predicted. Predictions are based on a model that accounts for the effects of DMI on starch and NDF digestibility, as described in the text. Note that although the methane production functions CH_4/ECM and CH_4/GEI appear linear over the range shown, they are in fact curvilinear, decreasing with increasing intakes.

that genetic selection for higher milk yields in dairy cattle has been accompanied by increased digestive capacity. No definitive research is available on whether the increased capacity is due to increases in rumen or total gastrointestinal tract volume, absorptive surface, changes in host-microbe interactions, or combinations of these effects. In dairy cattle diets, most of the decrease in DM digestibility observed as intake increases

Table 1. Summary of feeding management approaches to altering rumen fermentation and reducing CH_4 emissions per unit of ECM[1]

Feeding alteration	CH_4/ECM	Assumption(s) and comments
Increased DMI	Decreased 2 to 6% for each kilogram increase in DMI	(a) Increased fill; (b) increased rate of solids passage; (c) decreased rumen NDF digestibility will be compensated by increased hindgut NDF digestibility; (d) decreased rumen starch digestibility; (e) increased starch digestion in small intestine; (f) no difference in total-tract starch digestion; (g) increased production
Decreased forage particle size	Neutral	(a) Increased passage of forage particles from the rumen; (b) decreased rumen NDF digestibility will be compensated by increased hindgut NDF digestibility
Grain processing	Decreased 1 to 2.5% with 5% increase in apparent total-tract starch digestibility	(a) Decreased grain particle passage from rumen; (b) increased VFA yield with increased proportion of propionate; (c) no increase in intake of digestible DM (which may or may not be true)
Rumen pH <5.5	Decreased 15 to 20%	(a) Decreased rumen NDF digestibility not fully compensated for by hindgut fermentation; (b) assumes 50% reduction in apparent total-tract NDF digestibility; (c) milk yield reduced 10 to 15%; (d) no change in rumen starch digestibility and no effect on DMI
Increased concentrate feeding	Decreased 2% for every 1% increase in ration NFC; maximum reduction ~15%	(a) Effects manifested by less NDF fermented in total tract, shift of starch digestion from rumen to small intestine, and possibly lower rumen pH; (b) potential to increase intake; (c) higher proportions of propionate
Increased forage quality achieved by better management of harvesting and storage or pasture management	Decreased up to 5% with a 5 percentage unit increase in apparent total-tract NDF digestibility	(a) Increased yield of VFA (energy) is greater than increases in CH_4; (b) increased milk yield
Forage type/strain selection and genetics (e.g., brown midrib corn)	Decreased 0 to 4%	Improvements in digestibility lead to increased DMI, energy availability, and milk yields
Lipid feeding	Decreased 5% per unit of ether extract in ration	Potential for (a) decreased DMI, (b) decreased NDF digestibility, (c) decreased lactation performance, and (d) decreased milk components

[1]Many of the biological effects are interrelated and interdependent and, accordingly, the changes in enteric CH_4 emissions per unit of ECM (CH_4/ECM) are not likely to be additive. Expected decreases in CH_4/ECM range from 0 to 15%. These changes are modest because the range of alterations was restricted to what might reasonably be implemented or occur in commercial dairy production without compromising milk yield significantly (except as noted for rumen pH) compared with previously published reviews where the manipulations ranged from all-forage to all-concentrate diets for nonlactating and lactating animals. Manipulations that alter carbohydrate digestibility and thus energy availability will affect milk yield as well as CH_4 emissions.

is associated with a decrease in total-tract NDF digestibility, but not total-tract starch digestibility (Huhtanen et al., 2009), although starch digestion will be shifted from the rumen to the small intestine (Firkins et al., 2001). Huhtanen et al. (2009) predicted that for every kilogram increase in DMI, total-tract NDF digestibility is reduced $0.485 \pm 0.143\%$ for grass silages. Whether a similar reduction may be observed with NDF digestibility in legume or corn silages with increasing DMI is not known, but is presumed to be different. Assuming unchanged patterns of fermentation, the reduction in total-tract NDF digestibility with increasing DMI of the same diet will result in a proportional reduction in CH_4 emissions on a per-head-per-day basis.

Methane emission would also be expected to be affected by depression of ruminal starch digestibility with increasing intakes. Apparent ruminal starch digestibility was found to decrease linearly with increasing DMI by $1.21 \pm 0.59\%$/kg of DMI (Firkins et al., 2001). When ruminal starch digestibility is decreased, the majority of the starch passing out of the rumen will be digested in the small intestine rather than being fermented in the hindgut (Firkins et al., 2001; Huntington et al., 2006). In theory, intestinal digestion of starch should be more energetically favorable to the animal than ruminal fermentation to VFA, but in practice, no difference in energy availability has been demonstrated between the two (Huntington et al., 2006). With lower ruminal digestibility of NDF, more NDF will pass out of the rumen and be passed to the hindgut, where it can be fermented and produce CH_4. Although the decrease in total-tract NDF digestibility with increasing DMI is less than the decrease in ruminal starch digestibility, in terms of CH_4 production, the impact on NDF digestibility is expected to be larger because fermentation of hemicellulose and cellulose results in 2 to 5 times more CH_4 than fermentation of NFC (Moe and Tyrrell, 1979). The quantitative extent of the decrease in CH_4 emission with increasing DMI will depend on the proportions of starch and NDF in the diet and the proportions of cellulose and hemicellulose in the forages (legumes vs. grasses; further discussion in the next section).

Typically, the rate of passage increases with increasing DMI, decreasing the extent of ruminal degradation of the OM (Boadi et al., 2004). Associated CH_4 losses decrease by 0.77 to 1.6% GEI for each multiple or unit increase of intake (Johnson and Johnson, 1995; Beauchemin and McGinn, 2006a; Sauvant and Giger-Reverdin, 2009). The dairy NRC model (NRC, 2001) models the decrease in digestibility with increasing intake using the same discount factor for all feed nutrients (NDF, NFC, and CP). To account for the observation that the digestibility of all feed components are not equally depressed with increasing DMI, models are needed that allow for variable digestibility discount factors by individual nutrients. Also, interactions between intake level and diet composition exist in CH_4 as a proportion of gross energy (Sauvant and Giger-Reverdin, 2009). The relationships between digestibility, passage, and DMI are complex and have a major impact on rumen production of CH_4. Both the rate and the extent of rumen carbohydrate digestion determine the amount of CH_4 produced and the energy available for milk synthesis.

Type of Carbohydrates. Greater DMI with greater milk yields and lesser CH_4 yields are often achieved by feeding more digestible carbohydrates. The relative proportion of fermentation end products in the rumen, especially the VFA, is influenced by the proportion of NDF versus NFC in the ration (Moe and Tyrrell, 1979; Murphy et al., 1982; Sutton et al., 2003; Bannink et al., 2006). Forage-based diets high in cellulose, hemicellulose, and lignin favor production of acetate and butyrate (Moe and Tyrrell, 1979), whereas starch-based diets favor propionate production (Johnson and Johnson, 1995). Soluble sugars tend to stimulate greater proportions of butyrate and also increase fiber digestibility (Hindrichsen et al., 2005). However, selecting ryegrass forage for increased soluble carbohydrates did not reduce CH_4/ECM due to reduced NDF digestibility that negatively affected milk yield (Staerfl et al., 2012). In contrast, increasing NFC by altering the nonforage portion of the ration from 32 to 53% with corn grain, soybean meal, and whole roasted soybeans decreased CH_4/ECM by 20% in early-lactation cows (Aguerre et al., 2011).

Neutral detergent fiber is heterogeneous with respect to chemical composition, digestibility, and potential to produce CH_4. The highly digestible NDF in brewers and distillers by-products produces half to one-third of the CH_4 per kilogram of DM digested in vitro compared with forages with similar DM digestibilities (Johnson and Johnson, 1995). Given that distillers and brewers grains have high hemicellulose:cellulose ratios (1.5 to 1.6:1) compared with grasses (0.67:1) and legumes (0.35:1), this observation fits well with the Moe and Tyrrell (1979) equation, where digested hemicellulose produces only 37% CH_4 relative to digested cellulose. Cows fed increasing amounts of dried distillers grains with solubles that replaced corn and soybean meal emitted less CH_4 (g/d) and CH_4/ECM (Benchaar et al., 2013). In that study, changes in carbohydrate sources were confounded by treatment changes in diet lipid content sulfur intakes, and DMI. Tropical grasses (C4) tend to be less digestible than temperate (C3) forages due to their higher NDF content and greater lignification, and produce more CH_4 per unit of intake (Pinares-Patiño et al., 2009; Archimède et al., 2011). In contrast, tropical legumes are significantly less digestible and

produce less CH_4 per unit of intake than temperate legumes (Archimède et al., 2011). The greater content of tannins and other secondary metabolites in tropical legumes affects NDF digestibility and CH_4 production (Archimède et al., 2011); however, the authors did not use NDF digestibility in their analysis.

High-starch, cereal grain-based diets stimulate the growth and metabolic activity of propionate-producing microbes (Ominski and Wittenberg, 2005; Martin et al., 2010). Because the formation of propionate consumes reducing equivalents (Equation 3), enhancing propionate production reduces the amount of metabolic H_2 available for methanogenesis in the rumen. Ruminal pH also decreases with increasing NFC concentrations, which can inhibit the growth of methanogens and ciliate protozoa (van Kessel and Russell, 1996; Hegarty, 1999b). However, it can also reduce NDF digestibility. In general, decreasing the NDF:NFC ratio of ruminant diets can reduce the percentage of GEI lost as CH_4 (Beauchemin et al., 2008; Chagunda et al., 2009). Very low CH_4 emissions (2–3% GEI) are reported from cattle fed low- (10–30%) forage diets, such as beef finishing rations (Johnson and Johnson, 1995). Although in beef cattle research CH_4 is often expressed as percentage of GEI, it should be expressed as CH_4 per ADG or CH_4 per kilogram of carcass yield in an analogous manner to the CH_4/ECM approach for evaluating CH_4 emissions in dairy cattle. If grain supplementation increases GEI and ADG even though CH_4/GEI is unchanged, fewer days on feed will be required to reach target weight and less total CH_4 will be emitted during the growing and finishing periods. Accordingly, whole-farm GHG inventory models usually predict lower GHG emissions from on-farm animal and manure emissions and from off-farm feed production with increased grain and by-product feeding (Phetteplace et al., 2001; Lovett et al., 2006).

Although the word concentrates is broadly used many different feed ingredients can be incorporated into the nonforage portion of a ration. Hindrichsen et al. (2005) examined nonforage ingredients with lignified fiber, nonlignified fiber, pectin, fructans, sugar, or starch and found them to have differing effects on DM and NDF digestibilities, but not on CH_4 emissions when expressed as grams of CH_4 per kilogram of milk protein. Regression analysis of results from the same experiment (Hindrichsen et al., 2005) provided the following equation:

$$CH_4 \text{ (g/d)} = 91 + 50 \times \text{digested cellulose (kg/d)}$$
$$+ 40 \times \text{digested hemicellulose (kg/d)} + 24 \times \text{digested}$$
$$\text{starch (kg/d)} + 67 \times \text{digested sugars (kg/d)},$$

which can be compared with the equation from Moe and Tyrrell (1979):

$$CH_4 \text{ (g/d)} = 33.0 + 104.6 \times \text{digested cellulose (kg/d)}$$
$$+ 38.5 \times \text{digested hemicellulose (kg/d)} + 20.5$$
$$\times \text{digested neutral detergent-soluble residue (kg/d)}.$$

In both data sets, the digested cellulose and hemicellulose would be from combined forage and nonforage feed ingredients. In Moe and Tyrrell (1979), the neutral detergent-soluble residue fraction would include starch, sugars, silage acids, other organic acids, and the pectins and fructans not precipitated in NDF. Both equations clearly show that starch generates less CH_4 than hemicellulose or cellulose per unit digested. The high coefficient for sugars in Hindrichsen et al. (2005) may reflect the stimulatory effect of sugars on fiber digestion.

The difference in CH_4 produced per unit of starch versus cellulose is not a function of their chemical composition; both are hydrolyzed to glucose before being fermented. In contrast, hemicellulose, as a mixture of 5- and 6-C sugars, would be expected to result in a different VFA pattern and proportion of CH_4 than starch or cellulose. Rather than a chemical basis for the difference in CH_4 production between starch, hemicellulose, and cellulose, the difference appears to be a function of the microbial species that degrade and ferment the majority of each substrate (Hungate, 1966; Baldwin and Allison, 1983). Thus, as microbial species adapt to changing dietary substrates and rumen conditions, patterns of VFA and CH_4 production will change. Improving our understanding of the interrelationships between substrate availability and microbial maintenance and growth that affect overall rumen fermentation will lead to better predictions of CH_4 generation and identification of opportunities to manipulate fermentation and reduce CH_4 production. The observation that CH_4 production is influenced by associative factors between nutrient fractions in the diet implies that CH_4 can only be predicted for the diet or ration, not for the individual feed ingredients, which is analogous to the prediction of NE_L or MP (NRC, 2001).

Forage Quality, Species, Harvesting, and Storage. Leng (1993) estimated that 75% of global ruminant CH_4 emissions came from ruminants grazing low-quality feeds. Increasing the quality of the feed is an overarching concept related to feed efficiency and animal productivity, which can decrease CH_4 emissions per unit of product. Increasing forage quality is favorably received by livestock farmers because feeding high-quality forages is central to good farming practice and often increases profitability (Waghorn

and Clark, 2006). Forage quality can be improved by harvesting or grazing less mature forages, selection of genetic strains or species that have superior digestibility (e.g., brown midrib corn and sorghum), and proper storage, especially ensiling, to conserve digestible nutrient content, improve dietary utilization, and increase feed efficiency. In general, better-quality forages will contain a greater proportion of NSC to NDF or the NDF will be less lignified (Moss et al., 2000; Boadi et al., 2004).

Several studies have compared different forages in terms of CH_4 emissions (McCaughey et al., 1999; Boadi et al., 2002, 2004; Boadi and Wittenberg, 2002; Robertson and Waghorn, 2002; van Dorland et al., 2007; O'Neill et al., 2012). The diets compared legumes versus grasses, stage of maturity, and grazed versus harvested forages. However, some comparisons were confounded with other dietary changes to maintain energy density or nitrogen intakes. A comprehensive evaluation of the effect of forage quality on CH_4 emissions requires an approach that considers diet composition and level of intake. In essence, this has been done in the research to develop CH_4 prediction equations (Moe and Tyrrell, 1979; Mills et al., 2003) and in the meta-analysis of Archimède et al. (2011), which accounted for intake and NDF digestibility (discussed in the previous section).

The effects of forage preservation on CH_4 production have not been studied at length. The ensiling process results in fermentation of the forages, which can reduce digestion in the rumen (Boadi et al., 2004). Cows fed either a partial or total mixed ration with ensiled forages with OM digestibilities >80% had similar CH_4/ECM as cows consuming high-quality pasture with similar digestibilities (Robertson and Waghorn, 2002; O'Neill et al., 2012). When expressed as percentage of GEI, ensiled forages have been shown to produce less CH_4 than dried forages (Sundstol, 1981). Some evidence exists that maize and whole-crop small-grain silages will yield less CH_4 than grass silage, which likely reflects differences in carbohydrate composition and digestibility, but a need still exists for direct in vivo comparisons and whole-farm GHG analyses for all of these situations (Beauchemin et al., 2008). Different additives and inoculants have been added to silage with limited success in reducing CH_4 production (Boadi et al., 2004).

Feed Processing. Feed processing reduces the particle size distribution of the feed and alters the rates of fermentation and passage of the particles, with the benefit depending on the feed. Particles that are too small can pass undigested out of the rumen and will not increase the amount fermented (Russell and Hespell, 1981). Processing forages by grinding, chopping, or pelleting will decrease rumen NDF digestibility and can decrease CH_4 emissions as a result of increased passage rate (Table 1; Johnson et al., 1996; Moss et al., 2000) with decreased acetate:propionate ratios (Van Nevel and Demeyer, 1996). This effect is not usually evident with restricted intakes, but at high levels of intake CH_4 reductions of 20 to 40% per unit of DM could be achieved (Johnson and Johnson, 1995). Pelleting can decrease CH_4 production to a greater extent than chopping, but the effect of pelleting is most pronounced with low-quality forages (Hironaka et al., 1996). Also, the CH_4 reductions may not be great enough to justify the extra energy expenditure and the likely increased associated GHG production required to pellet the feed (Hironaka et al., 1996). Fine grinding of forages has proven to be uneconomical due to the greater incidence of acidosis associated with deficient effective NDF and decreased milk fat concentration (Boadi et al., 2004). Last, the acetate:propionate ratio has been decreased through alkali treatment of cereal straw (Van Nevel and Demeyer, 1996), a strategy that could reduce CH_4 by 10% (Johnson et al., 1996). Experimentation with feeding alkali-treated straw to sheep found CH_4 per unit of apparently digested OM to be reduced, and the volume of CH_4 produced per animal was significantly increased due to increased intakes (Moss et al., 1994). If alkali treatment of poor-quality forages were to be used for feeding cattle and digestibility were increased, CH_4/ECM or CH_4 per ADG would be expected to decrease.

Processing grains by grinding, rolling, or flaking can increase rumen fermentation and decrease the amount passing to the intestines (Table 1). Extensive rolling of barley increased DMI and maximized ruminal and postruminal digestibility of starch (Yang et al., 2001). Heat treatment through pelleting, flaking, extruding, and toasting can change the degradation rates of protein and carbohydrates and decrease the acetate:propionate ratio (Van Nevel and Demeyer, 1996) but the relationship with CH_4 emissions depends on the feed as well as composition of the total diet and intake.

Overall, processing could have mixed effects. Processing forages alters rumen fermentation and decreases rumen NDF digestibility. If NDF is digested in the hindgut or in manure storage, no net change in whole-farm CH_4 emissions will occur. Conversely, processing grains increases rumen DM and starch digestibility (Firkins et al., 2001), with more CH_4 being produced from rumen fermentation than if starch were digested in the small intestine, assuming no negative effects on fiber digestion. Processing that improves DM digestibility will reduce CH_4/ECM by increasing energy available for productive purposes and diluting CH_4 associated with maintenance. In contrast, processing that decreases digestibility and CH_4 per day per head is not desirable, as more feed inputs will be required to produce the same amount of milk.

Lipid and FA Supplementation. Lipid supplementation is an extensively researched enteric CH_4 mitigation strategy, and several reviews are available on this topic (Giger-Reverdin et al., 2003; Beauchemin et al., 2008; Eugene et al., 2008). Climate Change Central (2012) in Alberta, Canada already recognizes oil supplementation as a mitigation strategy under their protocols. The effect of dietary lipids on CH_4 production is dependent on the source, FA profile, inclusion rate (% of DMI), and diet composition (Beauchemin et al., 2007b; 2008). The form of the lipid supplement affects its availability in the rumen, and this appears to be more important than the FA profile (Beauchemin et al., 2009).

In vitro, lipid additives suppress ciliate protozoa (Dohme et al., 2000) and methanogen populations in the rumen (Machmüller and Kreuzer, 1999) by differing modes of action, depending on the primary FA (Dohme et al., 2001). They decrease OM and fiber degradability and reduce fermentable substrate (Van Nevel and Demeyer, 1996; Dong et al., 1997; Dohme et al., 2001; McGinn et al., 2004), which means less CH_4 production but is not a desirable effect in itself. Biohydrogenation of unsaturated FA can be an alternative sink for H_2, but this is trivial compared with methanogenesis (Johnson and Johnson, 1995; Hegarty, 1999a). In animals that are not rumen-fill limited but eat to meet energy requirements, lipids create a dilution effect because they replace fermentable carbohydrates in the energy supply. Also, they often reduce DMI. Finally, rumen inert or protected fats (such as calcium soaps) do not show the same effects as other lipid sources (Dohme et al., 2000). In a meta-analysis by Beauchemin et al. (2008) using 33 treatments, each 1% addition of fat to the diet resulted in a 5.6% reduction in CH_4 (g/kg of DMI) up to 36%. Another meta-analysis concluded that lipid supplementation to dairy cows reduces daily CH_4 production by 0.305 g/kg of DMI for each 1% increase in ration ether extract (**EE**), and mainly as a consequence of lower DMI (Eugene et al., 2008). The effect of lipid composition or type was not evaluated.

Given our focus on CH_4/ECM, we conducted a meta-analysis on the effects of lipid supplementation on CH_4 emissions. Eleven studies were identified in the published literature with different sources of lipid (whole seed, crushed seed, oils, calcium salts of FA, and FFA), and include the work of Andrew et al. (1991), Holter et al. (1992), Johnson et al. (2002), Dohme et al. (2004), Odongo et al. (2007b), Martin et al. (2008), Beauchemin et al. (2009), Hristov et al. (2009, 2011) Grainger et al. (2010), Mohammed et al. (2011), and Hollmann et al. (2012). Most of the studies were designed to compare different lipid sources; only 1 study used the same supplement at different levels (Hollmann et al., 2012). Often, more than 2 ingredients were different between treatments and nutrients other than EE varied between treatments within the same study. Five studies used open-circuit respiratory chambers, 1 study used hoods, and 5 studies used SF_6 methodology to measure CH_4 emissions. Measurement method was a significant effector of observed CH_4/ECM (data not shown). The data were analyzed using the following model:

$$y_k = \beta_0 + s_i + \beta_j \times ee + error_k,$$

where $y_k = CH_4$/ECM and are the treatment means (k = 1 to 35), $\beta_0 = $ a common intercept across studies, $s_i = $ the random study effect (i = 1 to 11), $\beta_j = $ the regression coefficient for the jth lipid source (j = 1 to 4), and ee = the EE content of the ration. Lipid sources were identified as either rumen inert (calcium salts of FA or stearic acid), oils (medium-chain FA or vegetable oils), seeds (whole, crushed, or extruded), or endogenous lipids in feedstuffs (control treatments). The standard error of CH_4 emissions across studies varied over a 3-fold range, and this variation was used to weight studies accordingly using the inverse of the reported standard error for CH_4 (g/d). The variance component due to the interaction between study effect and EE content was very small compared with the study effect and thus was removed from the model to improve parameter estimates.

Observed treatment means of CH_4/ECM as a function of ration EE content can be seen in Figure 4a, with lines connecting the individual treatment means within a study. Overall, a trend for decreasing CH_4/ECM could be seen as EE increased, although some studies showed little change (I, J, and K) or an increase (D and F). The differences between studies are large, and may be attributable to measurement method, diet, and animal characteristics, and other experimental variation, and all of these are captured in the study effect in the statistical analysis. After accounting for the study effect, the results show that increasing EE content in the ration reduced CH_4/ECM, and that significant differences existed in the interaction between lipid sources and EE content (Figure 4b). Each percentage unit of ration EE from inert, seed, oil, and endogenous lipid sources decreased CH_4/ECM by 0.78 ± 0.20, 0.71 ± 0.20, 1.12 ± 0.20, and 1.01 ± 0.38 g/kg, respectively. The slopes of inert and seed lipid sources were not significantly different from each other ($P > 0.48$), but differed significantly from the slope of oil lipid source ($P < 0.006$ and <0.002, respectively). The slope of endogenous lipid source was intermediate between that of inert and seed sources versus oil sources, and not

significantly different from any treatment ($P > 0.17$ to 0.51). The endogenous lipids in feedstuffs contain greater concentrations of MUFA and PUFA than SFA. The intermediate slope for endogenous lipid diets may be indicative of an effect of FA composition on rumen function and CH_4 production.

Different lipid sources may affect CH_4 emissions by altering DMI and this could affect CH_4/ECM. Previous reviews have observed a reduction in DMI with lipid supplementation (Chilliard, 1993; Allen, 2000; Beauchemin et al., 2008). In this analysis, the best fit model for DMI was $y_k = s_i + \beta_j + \beta_j \times ee + error_k$, with separate intercepts and slopes for each lipid source. Analysis of the effect of lipid source and ration EE content showed that inert and endogenous lipid sources did not affect DMI (kg/d; Figure 4c; $P > 0.85$ and $P > 0.77$, respectively). However, oil sources (vegetable oils and medium-chain FFA) significantly reduced DMI by 1.51 ± 0.40 kg per percentage unit increase in ration EE (Figure 4c; $P < 0.001$; intercept $= 28.0 \pm 3.10$). Seeds also reduced DMI by 0.90 ± 0.52 kg per percentage unit increase in ration EE (Figure 4c; $P < 0.09$, intercept $= 25.8 \pm 3.47$). This effect of ration EE for seeds followed a quadratic pattern, with reductions in DMI occurring at ration EE approximating 7% DM (Figure 4c). The greater variation observed with seeds is reasonable, given that these treatments included whole, crushed, and extruded seeds.

In summary, increasing ration EE with endogenous lipid in feedstuffs, inert lipids, or seed sources reduces enteric CH_4/ECM, and it appears that this is achieved by dilution of the fermentable carbohydrates in the DMI and potentially reduced DMI. No difference existed in CH_4/ECM between the inert, seed, or endogenous feed sources of lipids. Some seeds, vegetable oils, and medium-chain FFA further reduced CH_4/ECM, but it appears that this was largely achieved at the expense of reduced DMI, which could be detrimental to energy balance and milk yield over longer periods of time. Vegetable oils and medium-chain FA are known to alter rumen function and decrease NDF digestibility. Whether these lipid sources reduce enteric CH_4/ECM by this mechanism cannot be ascertained in this analysis, as rumen digestibilities were not measured. However, it is supported by subsequent research of Hollmann et al. (2013) that demonstrated reduced DMI and total-tract NDF digestibility with increasing dietary inclusion of coconut oil. Also, most of the studies used in this analysis were short-term feeding trials (2 to 5 wk), with the exception of Grainger et al. (2010; 12 wk). Future research in this area should focus on dose-response relationships by using multiple levels of lipid supplementation and longer-term trials where energy balance can be determined (Beauchemin et al., 2008; Grainger

et al., 2008b; Martin et al., 2008). Furthermore, the effect of lipid supplementation on emissions of CH_4 and other GHG must be evaluated on a whole-farm basis. If lipids reduce fiber digestibility, then more CH_4 may be emitted from the manure during storage and anaerobic fermentation (Hristov et al., 2013).

Typically, lactating cow rations contain 4 to 5% EE, with fat supplementation increasing levels to 5 to 7% DM. Current recommendations are for ration EE to not exceed 6 to 7% DM (NRC, 2001). With decreases in enteric CH_4/ECM of 0.71 to 1.21 g/kg for each percentage of ration EE and typical CH_4 emissions of 5 to 25 g/kg of ECM, a 2% increase in ration EE would be expected to decrease CH_4 approximately 10%. This reduction is comparable with the low end of the range of 10 to 25% reductions given on a CH_4/DM in Beauchemin et al. (2008). Reductions on a CH_4/ECM basis should be less than reductions on a CH_4/DM basis, given the strong, positive relationship between DMI and ECM. The effects of fat supplementation on milk and milk component yields are variable, and depend on the nutrient composition of the basal diet, FA composition of the endogenous and supplemental lipids, and stage of lactation as well the amount of fat supplemented (NRC, 2001). Excellent reviews on this topic can be found in Chilliard (1993), Jenkins (1997), and Schroeder et al. (2004).

Summary of Nutrition and Feeding Management Strategies. Many of these enteric CH_4 mitigation strategies are mechanistically geared toward enhancing the propionate:acetate ratio from fermentation. Although methanogens are a crucial part of the rumen ecology, CH_4 formation should be minimized and the yield of VFA maximized. The potential for reducing CH_4/ECM through nutrition and feeding management is modest (Figure 5) and will be mostly achieved by approaches that improve feed efficiency (Figure 6). Feeding nonstructural or starchy carbohydrates, high-quality forages at greater intake levels, or optimally processing the forages can reduce enteric CH_4/ECM emissions by 5 to 15% (Table 1; Figure 5).

It may be possible to combine some of the feeding and nutritional management approaches to reduce enteric CH_4/ECM (e.g., forage genetics and improved forage quality via management). Some of the approaches are redundant with respect to mechanisms and outcome (e.g., feeding more concentrate and reducing rumen pH <5.5). Some result in reduced DMI, which reduces both CH_4 and ECM, with no decrease or potentially increasing CH_4/ECM (e.g., decreasing rumen pH <5.5 or lipid feeding). Some approaches may lead to other undesirable outcomes, such as reduced feed efficiency, liver abscesses, and so on. With the redundancy in effects and the robust ability of the rumen microbes to
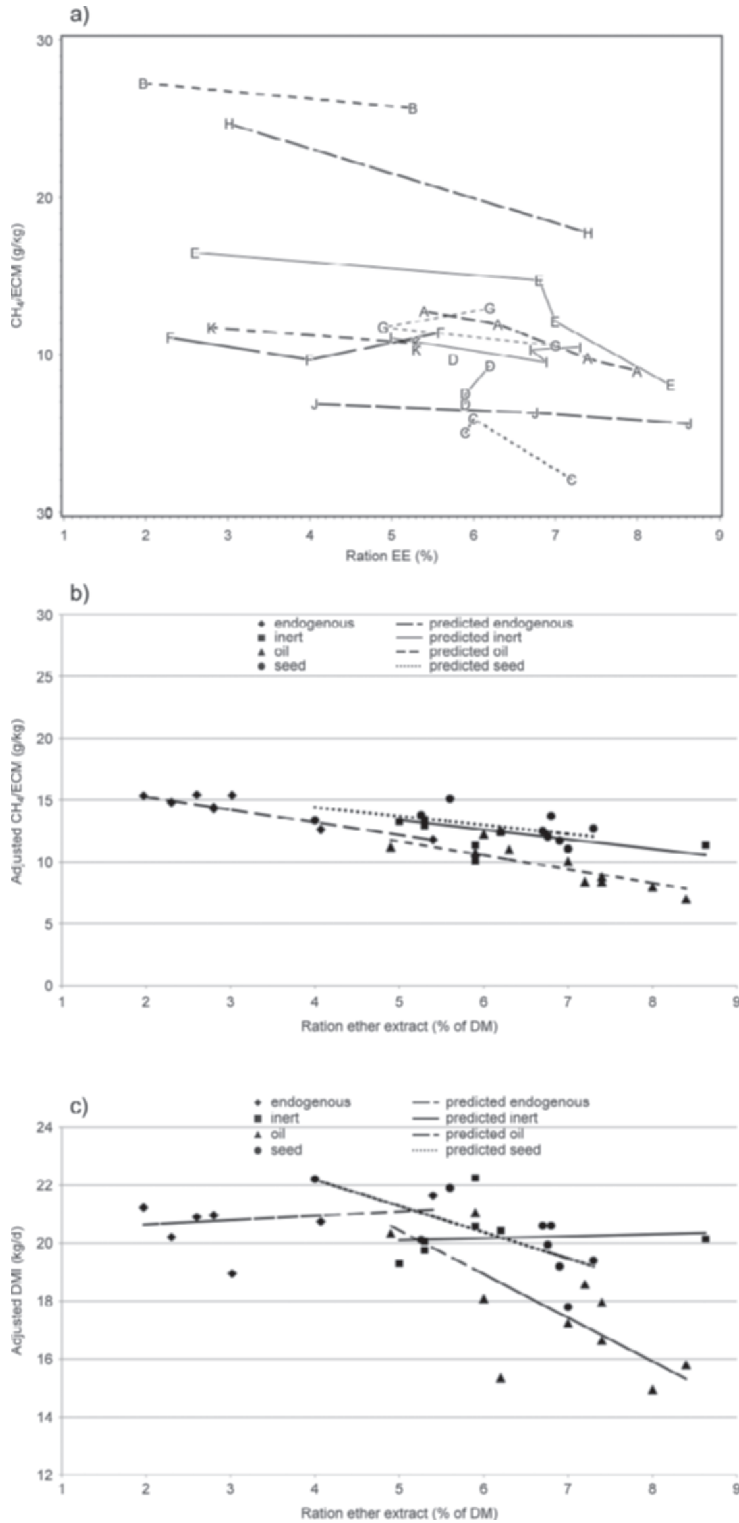
Figure 4. (a) Summary of enteric CH$_4$ emissions per unit of ECM (CH$_4$/ECM) as a function of ration ether extract (EE) content from 11 studies and 35 dietary treatments. Observed treatment means for each study are connected by lines. Study A: Hollmann et al. (2012), B: Grainger et al. (2010), C: Hristov et al. (2009), D: Hristov et al. (2011), E: Martin et al. (2008), F: Johnson et al. (2002), G: Dohme et al. (2004), H: Odongo et al. (2007a), I: Beauchemin et al. (2009) and Mohammed et al. (2011), J: Holter et al. (1992), and K: Andrew et al. (1991). (b) Predicted reductions in CH$_4$/ECM for inert, seed, oil, and endogenous (nonsupplemented) sources of lipid. Intercept = 17.25 ± 2.07 g/kg. Slopes for different lipid sources are given in the text. (c) Predicted reductions in DMI for inert, seed, oil, and endogenous (nonsupplemented) sources of lipid. Intercepts and slopes for different lipid sources are given in the text.
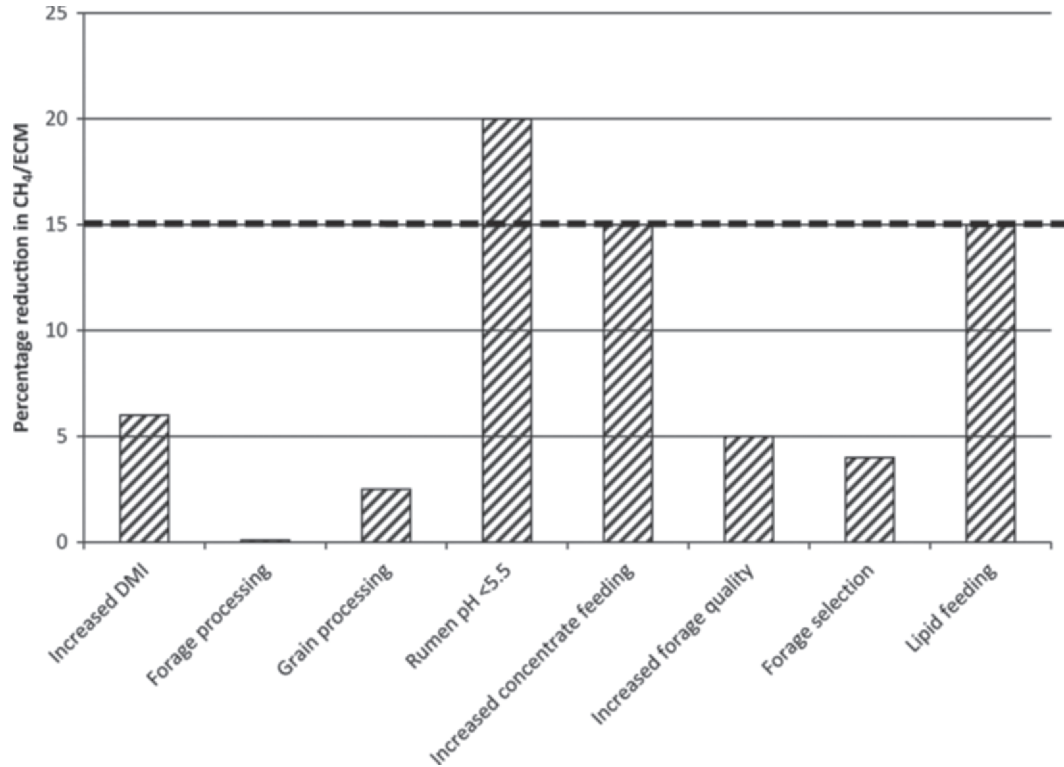
Figure 5. Feeding and nutritional approaches to reducing enteric CH_4 emissions per unit of ECM (CH_4/ECM) range from 0 to 15% and are largely nonadditive, with a maximum reduction of 15% or approximately 2.25 g of CH_4/kg of ECM.

adjust to changing conditions through several mechanisms, responses to different nutritional approaches are expected to be significantly less than fully additive (Figure 5). The implementation of many of the feeding and nutritional approaches is limited to lactating dairy cattle rations for practical or economic reasons and, thus, the reductions in enteric CH_4 would be less on a whole-herd basis than on an individual-cow basis.

Rumen Modifiers: Feed Additives and Biological Control

A wide variety of supplements exist that can be administered to reduce CH_4, such as chemical inhibitors, organic acids, and plant secondary compounds. The mode of action depends on the specific additive, but can include direct inhibition of methanogens or methanogenesis, suppression of ciliate protozoa, or providing or stimulating a competitive pathway for H_2 disposal. A wide variety of inhibitors have been studied, including halogenated CH_4 analogs, coenzyme-M analogs, and proton-motive force uncouplers (Czerkawski and Breckenridge, 1972; Martin and Macy, 1985).

In vitro, many additives and inhibitors suppress methanogenesis by 60 to 100% (Table 2). When these additives are fed to animals, however, the reduction in
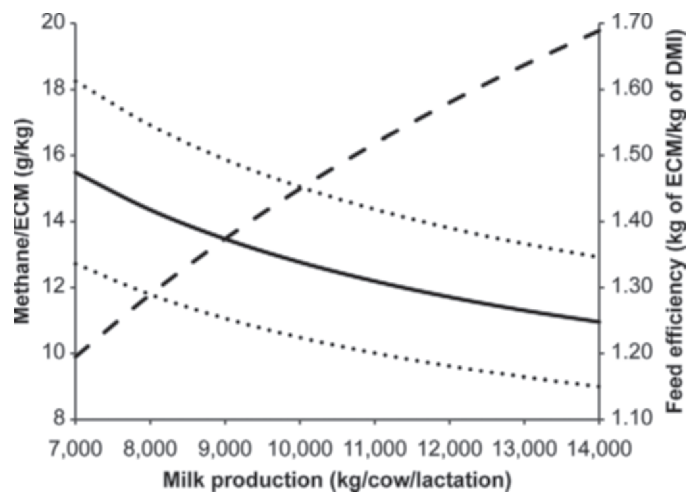
Figure 6. Enteric CH_4 emissions per unit of ECM (CH_4/ECM; solid and dotted lines, primary axis) decreases with increasing productivity and increasing feed efficiency (dashed line, secondary axis) and can vary by more than ±20%. Estimates do not consider improved diet quality or decreased digestibility for high-producing cows, which would further lower enteric CH_4/ECM. Predictions of CH_4 production were calculated as described in the text at Ym = 5.6% GEI (solid line) and at Ym= 4.6 and 6.6% (dotted lines, primary axis), where Ym = CH_4 as a percentage of gross energy intake (GEI).

CH_4 emissions has been either not evident or transient (<30 d; Table 3). Basic ecological principles need to be kept in mind when targeting microbial populations. With the incredible diversity of ruminal microbes, it is very likely that the removal or suppression of one group will result in another group adapting to fill its niche (Hungate, 1966; Czerkawski, 1986; Weimer, 1998). Recent studies indicate that CH_4 emission reductions resulting from short- and long-term defaunation do not correlate with the relative abundance of methanogens measured by quantitative PCR (Mosoni et al., 2011; Morgavi et al., 2012). In fact, Mosoni et al. (2011) reported that although defaunation reduced CH_4 emissions, ruminal methanogen density increased 10-fold. Second, if methanogenesis is reduced or eliminated, another route must exist for hydrogen disposal, or else rumen hydrogen concentrations will rise and potentially inhibit fermentation (Weimer, 1998). Ideally, this hydrogen or electron sink would result in the production of a compound that can be absorbed and metabolized by the animal so that the energy is not lost (Brown et al., 2011).

Several reviews have summarized the potential of using rumen modifiers on a qualitative basis (Van Nevel and Demeyer, 1996; Boadi et al., 2004, Beauchemin et al., 2008; Martin et al., 2010; Hristov et al., 2013). Many of these CH_4 reduction strategies have not been evaluated to determine the sustained effects of the additive, the appropriate in vivo dose, or the economics of the approach in terms of effect on milk production, all of which are important considerations for large-scale implementation. To date, no feed additives have demonstrated sustained reduction in CH_4 emissions without a negative effect on milk production in lactating dairy cattle other than the use of nitrate as an alternative electron acceptor, which has the issue of animal toxicity (Table 3; van Zijderveld et al., 2011). Successful biological control to reducing CH_4 emissions has been achieved with defaunation in sheep, goats, and growing cattle, but has had mixed effects on animal growth (Jouany, 1996). Given the extensive review of these strategies by others (above) and the focus in this review on quantitative reductions in CH_4/ECM, rumen modifiers will not be discussed further. At this time, greater opportunities exist in reducing enteric CH_4 emissions from dairy cattle through nutrition, feeding management, genetic selection, and improvements in herd health and productivity than with the use of feed additives as rumen modifiers (Waghorn, 2011). However, research should continue in identifying and developing rumen modifiers because of its value in elucidating rumen microbial interactions and increasing our knowledge of rumen function.

Table 2. Summary of rumen modifiers that have been tested in vitro but not in vivo[1]

Approach/compound	CH_4 reduction relative to control (%)	Effect on NDF digestibility	References	Comments
Electron acceptors (methylene blue, riboflavin, nicotinamide adenine dinucleotide, nitrate, sulfate, methyl- and benzyl viologen)			Reviewed in Van Nevel and Demeyer (1996)	Nonspecific action; function as alternative H_2 sinks; often required to be in stoichiometric proportions
Specific inhibitors of methanogenesis (p-aminobenzoic acid derivatives, mevastatin, lovastatin)	50–100		Dumitru et al. (2003); Machmüller et al. (2007)	
Bacteriocins (bovicin HC5)	50		Lee et al. (2002)	
Bacteriophage			McAllister and Newbold (2008)	High host specificity, but none identified that infect ruminal methanogens
Aspergillus oryzae	50	Yes	Frumholtz et al. (1989)	
Saccharomyces cerevisiae	10	Yes	Mutsvangwa et al. (1992)	
Exogenous fibrolytic enzymes	14–43	Yes	Dong et al. (1999); Giraldo et al. (2007a,b)	

[1]In addition to the references given, extensive reviews are available (Van Nevel and Demeyer, 1996; Moss et al., 2000; Boadi et al., 2004; Martin et al., 2010; Hristov et al., 2013).

Genetic Approaches to Increasing Productivity and Reducing CH4/ECM

Differences between individual animals in plant selection during grazing, rumen digesta retention rates, and host-microbe interactions may be heritable and thus amenable to genetic selection for animals with lesser enteric CH_4 emissions on a per-day or per-DMI basis (Pinares-Patiño et al., 2007; Clark, 2013; Ross et al., 2013). Poor repeatability of some CH_4 measurements and high within-animal variation may limit selection on this basis (Pinares-Patiño et al., 2007; Vlaming et al., 2008). Although genetic selection for reduced CH_4 emissions has been used in sheep and beef cattle (Hegarty and McEwan, 2010; Clark, 2013; Pinares-Patiño et al., 2013), the relationship between CH_4 emissions and animal growth has not been evaluated. Also, although metagenomic tools are being developed that may accelerate the selection process (Ross et al., 2013), to date no published evidence exists supporting the potential for this approach in dairy cattle, and by comparison with genetic selection for residual feed intake, it is likely to take more than 10 yr to develop.

Widespread consensus exists that increasing the productivity of an animal will decrease the proportion of CH_4 produced per unit of product (Johnson et al., 1996; Moss et al., 2000; Boadi et al., 2004; Beauchemin et al., 2008; Pinares-Patiño et al., 2009; Clark, 2013). The Environmental Protection Agency has clearly stated that "Improving livestock productivity so that less CH_4 is emitted per unit of product is the most promising and cost-effective technique for reducing emission" (EPA, 2005) and is in concordance with global efforts (Global Research Alliance on Agricultural Greenhouse Gases; Shafer et al., 2011). More-efficient dairy cows will produce more milk relative to the amount of feed ingested and energy lost as CH_4 (Figure 6). Production efficiency can be improved by genetic selection and management practices that address not only nutrition and feeding, but also reproduction, heat stress tolerance, disease incidence, culling rates, and heifer replacement programs. Although the effects of genetic selection and management improvements are commonly examined on an individual-cow basis, from a CH_4 mitigation perspective, it is more important to view them on a herd-productivity basis. Genetic selection and management approaches detailed below have the potential to increase yield while reducing the number of replacement animals needed, contributing to reduced CH_4 production by the herd and increased ECM.

Genetic Selection for Yield and Energetic Efficiency. Tremendous progress in genetic selection of dairy cattle has been made over the past 60 yr and,

combined with improvements in animal management, has resulted in a 400% increase in North American milk yields (Hansen, 2000; VanRaden, 2004; Shook, 2006; Capper et al., 2009). This increase in milk yield is paralleled by a corresponding 64% reduction in the US dairy cattle population and 57% reduction in CH_4 emitted per unit of product (Capper et al., 2009). Genetic selection has also increased milk yields in other countries and regions, including Argentina, Chile, Australia, New Zealand, Israel, and the European Union (Van Raden, 2004; FAOSTAT, 2014). Although remarkable gains have been made in milk yield through genetic selection, no indication exists that the genetic potential for milk yield is approaching a maximum (Cole and VanRaden, 2011). Cow-to-cow variation is large (SD = ±2,500 kg/lactation), indicating that substantial heterogeneity still exists in the population to permit selection.

On an individual-cow basis, CH_4/ECM can be reduced by 3 different approaches. The first is to increase milk yield per cow with correspondingly smaller increases in DMI, which dilutes the maintenance energy costs of the cow and increases gross energy efficiency. The second is to reduce body size without reducing yields of milk and milk components, which also has the effect of increasing gross energy efficiency, but by decreasing the maintenance energy requirements of the animal. The third is to select for residual feed intake or residual solids production, which are both measures of feed efficiency. These approaches are all based on the concept that maintenance energy is a fixed cost and a function of body size. Because CH_4 production is proportional to the energy intake of the animal, reducing the proportion of energy utilized for maintenance while maintaining or increasing milk yield would decrease CH_4/ECM.

Genetic selection over the past 6 decades has been based largely on the first approach, with increasing yields of milk and milk fat. Selection for yields of milk protein has been implemented over the past 2 decades in the US dairy industry. Reductions in enteric CH_4/ECM with genetic selection for milk yield follow a diminishing returns pattern (Figure 6). Predictions are based on a 680-kg Holstein cow producing milk with 3.7% milk fat and 3.0% true protein. Predictions for other breeds will follow a similar pattern, albeit at different milk yields. Dry matter intake was calculated using Equation 1-2 (NRC, 2001; page 4). Methane production was calculated at 3 levels of GEI that are within the range observed in the published literature and currently being used for US regional estimates by the Environmental Protection Agency (Kebreab et al., 2008; EPA, 2011b). Increases of 100 kg of milk per lactation are predicted to result in a 7.3% decrease in CH_4/ECM at a 7,000-kg

Table 3. Summary of rumen modifiers that have been tested in vivo[1]

Approach/compound	CH$_4$ reduction relative to control	Transient or sustained effect (>30 d)[2]	Animal toxicity	References	Comments
Monensin	4 to 10%	Sustained in one study; transient in the rest of the studies	None at recommended feeding levels	Callaway et al. (2003); Guan et al. (2006); Odongo et al. (2007a); Beauchemin et al. (2008)	CH$_4$ reductions achieved at feeding levels of 24 to 35 mg/kg (above feeding levels currently approved in the United States)
Monensin controlled-release capsules	0%	No effect	None	Moate et al. (1997); Grainger et al. (2008a); Waghorn et al. (2008)	One study was short-term (<14 d); the others were long-term (11 and ~29 wk)
Halogenated CH$_4$ analogs	80 to 100%	Sustained in 1 study; transient in the rest of the studies	Yes	McCrabb et al. (1997); Moss et al. (2000); Boadi et al. (2004); McAllister and Newbold (2008)	Reduced feed intake in beef cattle with improved feed efficiency
9,10-Anthraquinone	50%		Tissue residues	Kung et al. (2003)	
Dicarboxylic acids	50 to 75% in 1 study; 0% in others	Transient	Possible sodium toxicity if sodium salt is used	Moss et al. (2000); Boadi et al. (2004); McGinn et al. (2004); Mohammed et al. (2004b); Beauchemin and McGinn (2006b); Wallace et al. (2006); McAllister and Newbold (2008); Foley et al. (2009); Molano et al. (2008)	Also expensive
Essential oils	0 to 19%			Mohammed et al. (2004a); Beauchemin and McGinn (2006b)	May require encapsulation to slow volatilization; see also reviews by Calsamiglia et al. (2007) and Benchaar et al. (2008)
Saponins	0 to 16%			Hess et al. (2004); Santoso et al. (2004); Lila et al. (2005); Pen et al. (2007); Holtshausen et al. (2009); Wang et al. (2009)	Only short-term studies
Condensed tannins	12 to 46% in sheep and goats; 0% in beef cattle; 0 to 26% in dairy cattle		None	Woodward et al. (2002); Carulla et al. (2005); Hess et al. (2006); Beauchemin et al. (2007a); de Oliveira et al. (2007); Animut et al. (2008); Grainger et al. (2009)	Potential negative effect on protein nutrition, fiber digestibility, and milk yield; see also review by Waghorn (2008)
Nitrate and sulfate	16 to 57%	Sustained (1 study)	Yes	Sar et al. (2004); van Zijderveld et al. (2010, 2011)	As electron acceptors, these compounds have to be supplied in stoichiometric proportions, which may make them unrealistic (Weimer, 1998); risk of nitrite toxicity
Nitro-ethane and 2-nitropropanol	0% to 23% in steers	Transient		Anderson et al. (2004); Anderson et al. (2006); Gutierrez-Bañuelos et al. (2007); Anderson et al. (2008); Brown et al. (2011)	
Acetogens	100%	Sustained	None	Fonty et al. (2007)	Only demonstrated in gnotobiotically raised lambs; likely requires elimination of methanogens
Saccharomyces cerevisiae	0%		None	McGinn et al. (2004) Hristov et al. (2010); Chung et al. (2011)	
Direct-fed microbes	18%		None	Takahashi et al. (1997)	

Continued

Table 3 (Continued). Summary of rumen modifiers that have been tested in vivo[1]

Approach/compound	CH_4 reduction relative to control	Transient or sustained effect (>30 d)[2]	Animal toxicity	References	Comments
Defaunation	10 to 40%	Sustained	Yes	Morgavi et al. (2010); many others	Decreased NDF digestibility
Nisin	10%		None	Santoso et al. (2004)	
Immunization against methanogens	0 to 8%		None	Wright et al. (2004); Williams et al. (2008) Williams et al. (2009)	

[1]For sheep, goats, and beef cattle, CH_4 reduction is given as grams per head per day relative to the control and growth rates may or may not have been affected. For dairy cattle, CH_4 reduction is given as grams of CH_4 per kilogram of ECM relative to the control. Extensive reviews can be found in Van Nevel and Demeyer (1996), Boadi et al. (2004), Beauchemin et al. (2008), Martin et al. (2010), and Hristov et al. (2013).

[2]If cell is blank, the experiment was either not designed to test whether effect on CH_4 reduction was transient or sustained or the experiment was less than 30 d in duration.

production level, but only 3.1% decrease at a 13,000-kg production level, assuming no change in digestibility or rumen fermentation.

Although selection for reduced body size is theoretically possible, it has not been widely pursued. The ability to reduce body size while maintaining milk yield is limited due to the amount of feed that can be consumed by smaller animals. Also, a smaller animal contributes less to the beef supply. Currently in the United States, Holstein steers and culled dairy cows of all breeds account for 22% of domestically produced beef. In Europe, dairy animals account for 50% of the beef supply (Zehetmeier et al., 2012) and worldwide, meat from dairy breed animals is estimated to be 57% of the beef supply (FAO, 2010).

Although it is often speculated in the dairy industry that Jersey cows are more energy efficient than Holsteins due to their smaller body sizes and higher content of milk solids, the research literature does not generally support this concept. Research on energy metabolism of mature Jersey and Holstein cows did not show any breed differences for maintenance and production requirements per unit of metabolic BW ($BW^{0.75}$; Tyrrell et al., 1991). Consequently, CH_4 production per unit of milk was not different between the 2 breeds. In a 3-breed comparison with direct measurements of CH_4 and milk production, no differences were found between Jerseys and Holsteins in CH_4 per DMI or CH_4/ECM (Münger and Kreuzer, 2006). The third breed, Simmental, had similar CH_4 per DMI but more CH_4/ECM during lactation as a consequence of the lower milk production as a proportion of body size and correspondingly greater proportion of CH_4 associated with maintenance (Münger and Kreuzer, 2006). In contrast, in recent cross-breeding experiments, first-lactation Jersey cows produced more ECM per unit of metabolic BW than Holsteins and Jersey-Holstein first-generation (F1) crosses (Olson et al., 2010). However, it appears that the Jerseys were more physiologically mature at calving than the Holsteins and did not use as much energy in support of growth during the first lactation. Whether this breed difference in energy efficiency would continue into the second-and-greater lactations is unknown and would require further study.

Residual feed intake (**RFI**) and residual solids production (**RSP**) are related approaches in which cows are genetically selected for those that are more efficient in using feed nutrients to synthesis milk components at a fixed body size (Herd and Arthur, 2009; Coleman et al., 2010). Dilution of maintenance costs is implicit in both approaches. Residual feed intake follows a normal distribution, which improves its utility for conventional genetic selection compared with feed efficiency (kg of ECM/kg of DMI), which is usually not normally dis-

tributed (St-Pierre and Thraen, 1999). Although the genetic and physiological basis of RFI is sound (Herd and Arthur, 2009), applying RFI to dairy cattle has some concerns because of the high correlation between DMI and BW and the sensitivity of the estimate to the measurement period during lactation (Coleman et al., 2010).

Heritabilities for RFI in dairy cattle have been estimated at 0.01 to 0.40 (Coleman et al., 2010; de Haas et al., 2011; Connor et al., 2012; Basarab et al., 2013). Some of these heritabilities may be overestimated, as they were determined in single herds. Also, the genetic variation in RFI is <15% in dairy cattle (Coleman et al., 2010), thus limiting the magnitude of the potential for reductions in enteric CH_4/ECM to <5%. Altered digestibility does not appear to be a major contributor to differences in RFI and RSP between cows (Coleman et al., 2010; Waghorn and Hegarty, 2011). An exception was reported by Rius et al. (2012), where a tendency toward increased DM and OM digestibility was observed in first-lactation animals that had been selected for negative RFI as growing heifers, although no difference in DMI existed during the short lactation trial. Using RFI or RSP in a selection index will reduce enteric CH_4/ECM in direct proportion to the reduction in DMI or increase in milk solids yield (e.g., a 1% reduction in DMI or 1% increase in milk solids will reduce CH_4/ECM by 1%), with the assumption that digestibility has not been affected.

Lifetime Production. Last, genetic approaches that improve health, disease resistance, reproduction, and tolerance to heat stress will lead to increases in individual lifetime and herd productivity and indirectly reduce CH_4 emissions per unit of milk. Incidences of common diseases in dairy cattle have low to moderate heritabilities (h^2 = 0.05 to 0.25; Uribe et al., 1995; Zwald et al., 2004) and are positively associated with selection for increased milk production (Rauw et al., 1998). Tolerance to heat stress is also heritable (Ravagnolo and Misztal, 2000). During the past decade, selection indexes for dairy cattle have been modified to include reproductive traits, susceptibility to mastitis, and productive life (lifetime net merit index; VanRaden, 2004), all of which will increase the efficiency of milk production and further reduce CH_4 emissions if used by dairy producers. Genetic selection for ECM has been demonstrated to reduce CH_4/ECM by 15% for the first 3 lactations until mature size and maximum milk yield are achieved (Bell et al., 2011).

In summary, genetic selection for milk yield, energy efficiency with either RFI or RSP, disease resistance, and heat tolerance will result in reductions in enteric CH_4/ECM through increased milk yield, dilution of maintenance feed costs, and reduced need for replace-
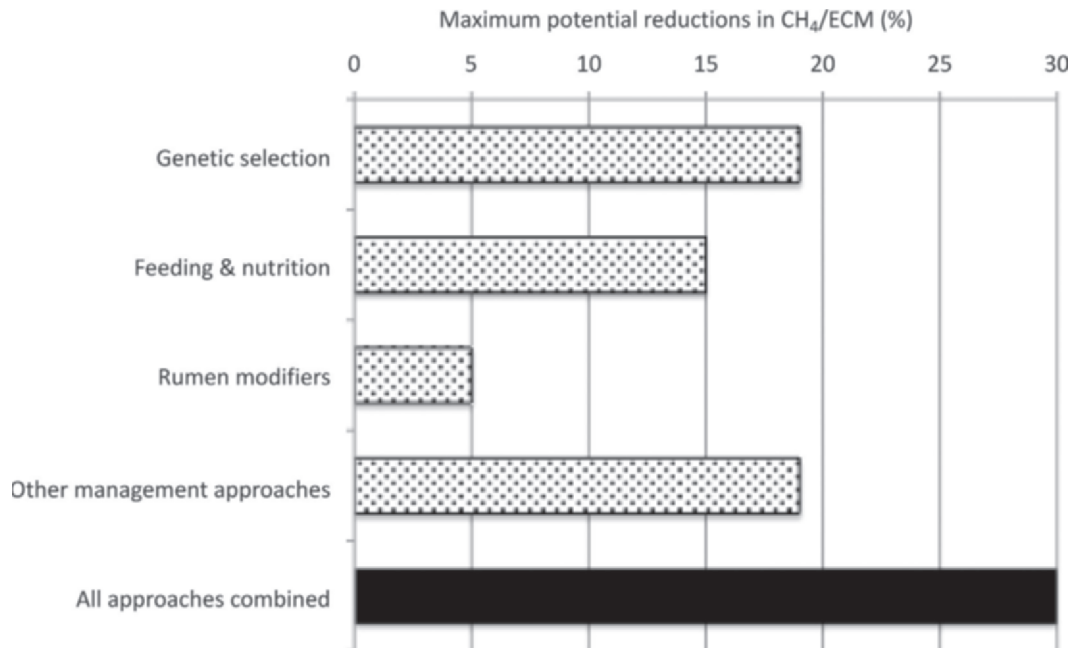
Figure 7. Estimated maximum impact of various approaches to mitigating CH_4 in intensive dairy production that have been demonstrated to be effective on an in vivo basis. Approaches are not expected to be fully additive; lower additivity would reduce impacts in each category. Detailed information on the estimates for each category is provided in the respective sections of the text.

Table 4. Reducing age at first calving and culling frequency reduces the number of replacements needed and enteric CH_4 emissions per unit of ECM (CH_4/ECM) at the herd level

Culling rate (%)	Age at first calving (mo)			
	22	24	26	28
	No. of replacements needed per 100 cows[1]			
25	54	59	64	69
30	65	71	76	82
35	75	82	89	96
40	86	94	102	110
	Replacement contributions to whole-herd enteric CH_4[2] (%)			
25	19.6	21.0	22.4	23.7
30	22.7	24.2	25.7	27.2
35	25.5	27.2	28.8	30.3
40	28.1	29.9	31.6	33.2

[1]Calculated from St-Pierre (1998), based on 5% of heifers born dead on arrival and 10% culling and mortality.
[2]Calculated based on number of replacement heifers required; lactating cows with mature BW = 680 kg, producing 31.8 kg of ECM; DMI calculated according to NRC (2001); and methane production = 5.6% gross energy intake for lactating cows, 7.0% for nonlactating mature cows, and 8.0% for replacement heifers.

ment animals. The biological bases of some of these approaches are redundant, and they would not be expected to fully additive. The combined impact of these genetic approaches in intensive dairy operations on reducing enteric CH_4/ECM is estimated to be 9 to 19% (Figure 7), with part of it being manifested at the individual cow level (milk yield; Figure 6) and part through reductions at the herd level (lower culling and fewer replacement animals; Table 4). Although genomic approaches give promise of being able to capitalize on the heritable, between-animal variation in enteric CH_4 production (g/d) as a genetic selection approach, they have not yet been developed to the point of demonstrating actual CH_4/ECM reductions in dairy cattle. Also, the results of genetic selection are permanent, unlike management approaches, but must be supported by adequate management to achieve the desired reductions in enteric CH_4/ECM.

Management Approaches to Improve Productivity and Reduce CH₄/ECM

Approximately 50 to 55% of the increase in milk yields under intensive management has been achieved by genetic selection, and the remainder through improvements in management practices (Hansen, 2000; VanRaden, 2004; Shook, 2006). Animals cannot reach their full genetic potential if factors in their environment are limiting. Currently, a wide range in herd average milk yields exists, which reflects the variation in genetic potential and the variation in environment, which is altered by management practices. Herd production averages in the United Kingdom and United States range from 50 to 150% of the average, with individual animals recorded at >350% of the average

(Wall et al., 2012; R. A. Cady, Elanco Animal Health, Greenfield, IN, personal communication; Holstein Association, 2013).

Management practices that enhance the ability of individual cows to increase milk yields and reach their genetic potential will reduce the amount of CH_4/ECM in the whole herd. These management approaches may include practices to reduce nonvoluntary culling and diseases, facility and equipment designs to improve the cows' environment, and use of performance-enhancing technologies [e.g., recombinant bST (**rbST**)] as well as improvements in nutrition and feed delivery. All of these approaches have potential to improve profitability as well as decrease CH_4 emissions (Knapp et al., 2011).

Heat Stress Abatement. Animal responses to heat stress include reduced DMI, decreased average daily gain, decreased milk yield, and decreased fertility and poor reproduction (Kadzere et al., 2002; Hansen, 2007). Heat stress also contributes to increased culling and death losses (St-Pierre et al., 2004). During heat stress, milk production is decreased more than DMI, which increases CH_4/ECM (Rhoads et al., 2009). It may not be the extent of heat stress alone that affects animals, but also the duration of the heat stress (Hubbard et al., 1999; St-Pierre et al., 2004). This is supported by anecdotal evidence from the dairy industry, where it is commonly observed that adequate night cooling reduces the impact of heat stress during multiple-day periods of elevated temperature and humidity.

The minimum threshold where animals begin experiencing heat stress is considered to be a function of production level (Bouraoui et al., 2002; Kadzere et al., 2002; St-Pierre et al., 2004; Zimbelman, 2008). Endogenous heat production increases with the increased DMI and metabolism associated with increased milk yields

(Kadzere et al., 2002). Ravagnolo and Misztal (2000) found a negative genetic correlation (r = −0.36) between the heritability for milk yield and heat tolerance. This finding suggests that as dairy cattle have been selected for improved milk yields, their tolerance to heat stress has decreased. A 25% improvement in heat stress tolerance is estimated to reduce culling by 2.5%, deaths by 0.5%, and milk production losses by 1,000 kg/cow per year, with a net reduction in CH_4/ECM of 10% in intensive dairy systems (St-Pierre et al., 2004; Table 4; Figure 7). An additional consideration with regard to environmental sustainability is that current management approaches for heat stress abatement use large amounts of water to enhance evaporative cooling and require electricity to pump water and run fans. Strategies that reduce or eliminate water and fan use in heat abatement may have substantial economic as well as environmental sustainability value in the future.

Disease in the Transition Period. One of the most challenging areas in dairy cattle management is the transition period from gestation to lactation. The highest incidence of metabolic and infectious diseases is seen in the first 60 d postcalving, with corresponding high rates of culling, death, and loss of lifetime production (De Vries, 2004; Hadley et al., 2006; Overton and Fetrow, 2008). Across all stages of lactation, culling for disease and lameness accounts for 20% of all culling (Godden et al., 2003; Hadley et al., 2006). Many of the diseases that occur during the transition period are interrelated, and a cow that experiences one disease is more likely to experience additional diseases (Curtis et al., 1985; Burhans et al., 2003). Also, cows that experience disease early in the lactation are more likely to have poor production and poor reproduction, with increased days open and increased services per conception (Schrick et al., 2001). During the transition period, cows are more sensitive to heat stress, resulting in poor milk production and poor reproduction (De Vries, 2004). Management improvements that decrease the incidence of infectious disease and metabolic disorders during the transition period will decrease involuntary culling and death loss, and increase individual cow productivity. A 5% reduction in culling for disease during this period, combined with increased milk yields of 1,000 kg/cow per year, is estimated to reduce whole-herd emissions by 8 to 12% (CH_4/ECM; Table 4; Figure 7).

Production-Enhancing Agents. Ionophores, direct-fed microbes, enzymes, and rbST are available for use in the United States. These products increase feed efficiency, buffer ruminal pH to prevent acidosis, inhibit unwanted microbes or stimulate beneficial microbes in the rumen, accelerate growth, and increase milk yields. By doing this, production is enhanced and CH_4 emissions generally decrease per unit of product.

Recombinant bST reduces maintenance inputs relative to production output, making more efficient use of dietary energy and protein to meet milk production requirements (Bauman, 1992; Baldwin and Knapp, 1993; Capper et al., 2008). Johnson et al. (1992) estimated that increasing productivity by 13% through use of rbST would result in a 9% decrease in CH_4 emissions in a herd on a per-day or per-year basis. Furthermore, modeling indicates that rbST-treated dairy herds have less whole-farm GHG emissions and an overall reduced impact on the environment, compared with the same production from conventional or organic dairy farms (Capper et al., 2008).

Fertility. Reproduction is obligatory in all domestic livestock species (Flowers, 2013). For dairy cattle, gestation and lactation overlap; cows ideally become pregnant 3 to 4 mo after calving and beginning the current lactation. Although declining fertility in dairy cattle, particularly in North American Holsteins, has been a concern (Hansen, 2000; Lucy, 2001; LeBlanc, 2013), indications are that this trend has been stalled or reversed (USDA, 2012). Reproductive efficiency affects dairy farm profitability (De Vries, 2006) because cows in well-managed reproduction programs spend more time in the highest-yielding part of their lactations and have longer productive lifetimes. Also, fewer replacement animals are needed in herds with better reproduction rates (Table 4).

Approximately 19% of culling decisions are for reproductive reasons (Hadley et al., 2006). A reduction in culling due to poor reproduction from 35 to 30% is estimated to reduce whole-herd enteric CH_4 emissions by 3.1% when age at first calving is 26 mo. This estimate does not include the improvement in lifetime productivity that accompanies improvements in reproduction. Additionally, dairy profitability is improved by reducing days open that are beyond the optimum (Groenendaal et al., 2004; De Vries, 2006). The economic value of reduced days open is not only a function of the mean days open but also of its variance.

### Reducing the Number of Dry Cows and Replacement Heifers

Reduced culling reduces the requirement for replacement animals and is an immediately effective approach to reduce CH_4/ECM and increase dairy profitability. The improvements in genetic selection and management discussed above and in Knapp et al. (2011) can further augment efforts to reduce CH_4/ECM on a herd basis. The number of dry cows in a herd is largely a reflection of the effectiveness of the reproduction program used. Good reproduction management will result in an optimal dry period length for individual cows

that is a balance between having a minimum dry period that allows mammary tissue to involute and regenerate to achieve good production in the following lactation versus having too long a period with no production. Effective reproduction programs will also effectively increase milk per cow by having cows spend more of their productive days in the higher-producing periods of the lactation production cycle (De Vries, 2006; Wall et al., 2012). Similarly, extended lactations are not predicted to reduce CH_4/ECM because of lower milk yields in late lactation (Wall et al., 2012).

With replacement heifers, the number needed is a function of culling of the older cows in the lactating herd, age at first calving, heifer mortality and culling, and farm goals for expansion (Table 4). Reducing the age at first calving for properly developed heifers will reduce the energy requirements during the growing period, which is a non-milk productive period that contributes substantially to the maintenance energy required by the herd. Decreasing mortality and morbidity rates also has a significant effect on CH_4 reduction because animals that die or are culled before their first lactation represent a significant use of energy and resources without any usable food being produced. Lower culling levels, reduced age at first calving, and reduced heifer mortality would reduce the number of replacement heifers needed, and this would be accompanied by

a corresponding, but smaller, decrease in CH_4 emissions by the whole herd (Table 4; Figure 7). These estimates are in accordance with estimates for United Kingdom herds, where the replacement stock accounted for 21 to 26% of whole-herd enteric CH_4 emissions (Wall et al., 2012). For example, reducing culling from 35 to 30% and age at first calving from 26 to 24 mo at the same herd average milk yield would decrease enteric CH_4 contributed by the replacement animals to whole-herd emissions by 4.6% (Table 4).

However, culling levels that are too low compromise genetic progress from generation to generation, and heifers calving too young (<21 mo) result in lower lifetime production (Gill and Allaire, 1976). Reducing heifer mortality and culling results in an equal reduction in the proportion of heifers needed as replacements (i.e., a 5% reduction in heifer mortality and culling translates into 5% less heifers needed) and provides a substantial opportunity for the dairy industry to reduce CH_4 emissions while improving animal welfare (Figure 7). However, reducing culling of heifers and mature cows will decrease the amount of beef contributed by the dairy industry and would require an increase in beef animals to maintain the same national or global supply. Also, beef from dairy animals produces significantly less GHG per kilogram of meat than meat produced either in feedlot or extensive production systems, due
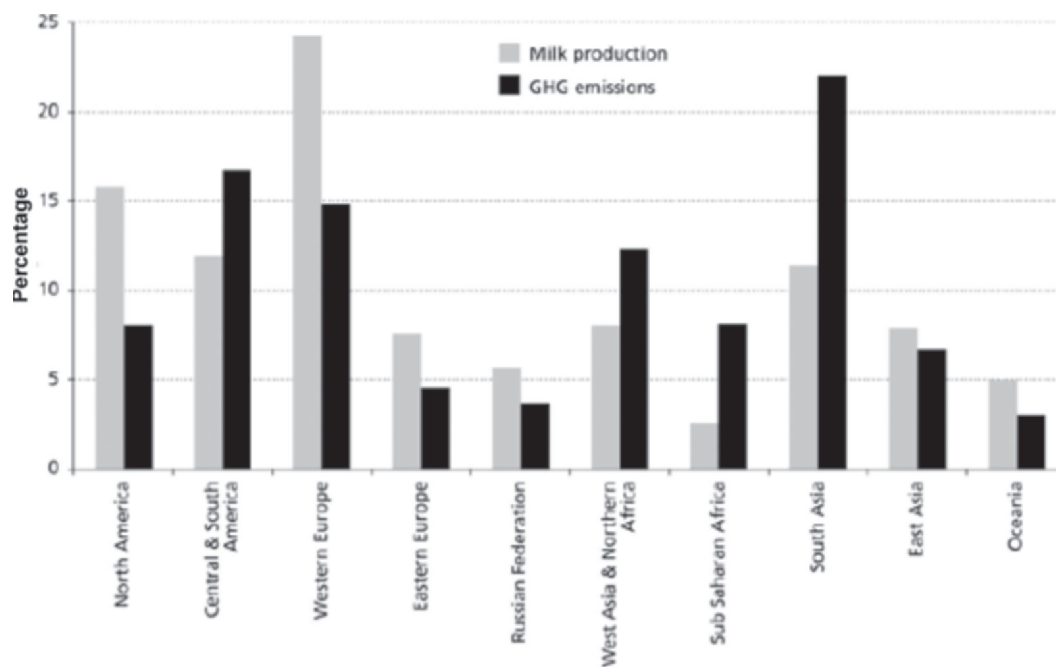
Figure 8. Intensive dairy production in developed countries contributes less greenhouse gas (GHG) emissions per unit of ECM than extensive systems in developing countries. Emissions and production for each region given as percentage of global total. Global milk production was 553 million tonnes, meat from dairy animals was 37 million tonnes, and GHG emissions associated with dairy production (milk and meat) were 1,969 million tonnes of CO_2 equivalents [CO_2e; 2007 estimates; from FAO (2010); reprinted with permission from the Food and Agriculture Organization of the United Nations (FAO)].

to the dual-product nature of dairying ($<$10 vs. 15 to 70 kg of CO_2e/kg of meat; FAO, 2010; Zehetmeier et al., 2012; Gerber et al., 2013).

In summary, management approaches other than nutrition and feeding, including heat stress abatement, disease control and treatment, performance enhancing technologies, and reproductive management can increase milk yields and reduce culling and the need for replacement animals. Several of these approaches are additive, although they may not be fully so. These improvements in animal and herd performance are estimated to lower enteric CH_4/ECM by 9 to 19%, depending on the genetic potential of the cows (Figure 7).

Potential for Reducing CH₄ Emissions from Dairy Production Around the World

On a global basis, GHG emissions estimated in life-cycle assessments of dairy production vary by country from 1 to 7.5 kg of CO_2e/kg of ECM, with an average of 2.4 $\pm$ 0.6 kg of CO_2e/kg of ECM (FAO, 2010; Hagemann et al., 2011), of which only a part is enteric CH_4. Of the GHG emissions, 67% was attributed to milk and 33% to meat (FAO, 2010). The estimate of GHG per kilogram of meat is very sensitive to the allocation basis (product mass vs. protein content vs. economic value), whereas GHG/ECM is less so (FAO, 2010; Hagemann et al., 2011; Mc Geough et al., 2012; Zehetmeier et al., 2012). Meat from dairy animals was estimated to contribute 57% of the global beef production and 13% of global livestock and poultry meat production (FAO, 2010). Intensively managed dairy production systems in developed countries contribute the least CO_2e/ECM, whereas extensive production systems in developing countries have the highest (Figure 8; FAO, 2010; Hagemann et al., 2011). Globally, on-farm emissions were estimated to be 93% of total GHG emissions in dairy production, and included CO_2 from fuel and electricity usage, CH_4 from enteric and manure fermentation, and N_2O from crop fertilization and manure (FAO, 2010). However, enteric CH_4 and on-farm GHG emissions from dairy production contribute only approximately 25 and 70%, respectively, in developed countries where more emissions associated with off-farm feed production and postharvest processing and consumption occur (Gill et al., 2010; Thoma et al., 2013).

The conservative estimates in this analysis suggest that reductions of 15 to 30% in enteric CH_4/ECM can be achieved in intensive dairy operations using combinations of several strategies (Figure 7). These estimates are somewhat less than estimates in the analysis by Gerber et al. (2013), likely due to an emphasis on systems that currently attain high levels of animal productivity and the recognition that few of the approaches will be fully additive. Most of these approaches are not novel, but they are proven. They are the results of decades of research in genetics, microbiology, nutrition, physiology, and veterinary medicine from scientists around the world. Also, they underlay the 5-fold difference in GHG/ECM emissions between intensive operations, including confinement housing and intensively managed grazing dairies, and extensive dairy operations. The upper end of the estimated reductions in this analysis, largely based on confinement housing, is not significantly different than the estimate of 27 to 32% improvement in GHG per hectare for managed grazing where milk yield per hectare was held constant (Beukes et al., 2010), reinforcing the idea that concepts underlying CH_4 mitigation via improvements in production efficiency have been and can be applied to different management systems as appropriate (Waghorn, 2011). To continue achieving gains in animal productivity requires a shift from focusing solely on milk or milk component yields to adding an emphasis on traits to enhance lifetime productivity and feed efficiency. This emerging paradigm is being implemented in genetics by the addition of traits for lifetime productivity and residual feed intake in selection indexes in several countries. Cattle management, including nutrition, reproduction, health, and facility design will need to continue improving to support the genetic progress.

Significantly more opportunity exists in extensive systems to reduce CH_4/ECM through combinations of genetic selection, forage production, nutrition, and other management approaches (FAO, 2010; Gerber et al., 2013). The scientific basis for these improvements already exists; achieving them depends on economics, government policy, and cultural considerations (Gerber et al., 2013). The approaches discussed in this review can be implemented in any country or region and will benefit dairy production. A more detailed discussion of regional GHG mitigation opportunities can be found in Gerber et al. (2013).

Several countries, especially New Zealand, Australia, Canada, and the Netherlands, have invested heavily in CH_4 abatement research in livestock through their agricultural research institutions, and private industry is also contributing. Since 2002, New Zealand has made a concerted effort to identify CH_4 mitigation strategies through the formation of the Pastoral Greenhouse Gas Research Consortium (PGgRc; http://www.pggrc.co.nz). Several international scientific organizations have been established to further collaboration and capitalize on synergies between research groups, including the Global Research Alliance (http://www.globalresearchalliance.org) and Livestock Emissions and Abatement Research Network (LEARN; http://www.livestockemissions.net). Achieving substantial im-

provements in dairy cattle productivity and reductions in emissions of CH_4/ECM basis requires the collaboration of scientists from multiple disciplines, including agronomy and soil science, economics, engineering, genetics, nutrition, reproductive physiology, and veterinary medicine.

CONCLUSIONS

Research in genetics, health, microbiology, nutrition, and physiology and application of the results to dairy production have led to tremendous improvements in animal performance over the past century. These improvements provide a growing supply of milk that minimizes the environmental impact of GHG emissions from dairy cattle. Continued application of these approaches to dairy production as well as research and development of novel methods can further reduce enteric CH_4 and other GHG per unit of product while increasing the milk supply needed to meet the anticipated 58% increase in global dairy demand by 2050 (FAO, 2011).

Genetic selection for feed efficiency, heat tolerance, disease resistance, and fertility can augment selection for milk yield in reducing enteric CH_4/ECM with the potential of 9 to 19% reductions (Figure 7). To achieve enteric CH_4/ECM reductions through genetic selection requires appropriate supporting management, including feeding and nutrition, health, reproduction, and housing facility design. Feeding and nutrition have modest (2.5 to 15%) potential to mitigate enteric CH_4/ECM in intensive dairy operations in developed countries, with significantly more potential when combined with crop and forage production in developing countries (Figure 7; FAO, 2010; Gerber et al., 2013). Impacts of feeding and nutrition will be mostly achieved by approaches that improve feed efficiency. Feed additives, chemical inhibitors, and biological approaches to altering methanogen populations, activities, and rumen fermentation cannot compromise rumen digestibility and fermentation if they are to be viable CH_4-reduction approaches. To date, rumen modifiers other than nitrates have not shown sustained reductions in CH_4/ECM. Feeding approaches and rumen modifiers that shift digestion to the hindgut or to manure in storage will not result in net reductions in CH_4 emissions at the farm level. Improvements in estrus detection, estrus synchronization, prevention of early embryonic death, heat stress abatement, and transition cow health would result in improvements in reproduction, reduce the number of cows culled due to poor reproduction and disease, and reduce the number of replacement animals needed. These management approaches could reduce enteric CH_4/ECM by 9 to 19% (Figure 7).

Recognizing that genetic and management mitigation approaches presented in this review will not be fully additive and some cannot be applied to the whole herd in a dairy operation, we estimate that their combined potential to reduce enteric CH_4/ECM is 15 to 30% in intensively managed dairy production systems that are already achieving high animal performance. Implementation of any strategy to mitigate enteric CH_4 must consider the impact on other GHG emissions from the dairy production unit and the impact on other agricultural sectors, especially beef production. Adoption of mitigation strategies by dairy producers will depend on these considerations as well as the feasibility of implementation, economic impact, and regulatory policy.

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