The impact of improving feed efficiency on the environmental impact of livestock production

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Publisher statement: Recent IPCC reports have highlighted the environmental impact of livestock production as a major source of non-CO_2 emissions: methane (CH_4), nitrous oxide (N_2O) and ammonia (NH_3). The livestock sector must react to these reports and develop or implement methods that can reduce greenhouse (GHG) emissions from livestock production. Reducing greenhouse gas emissions from livestock production provides authoritative reviews on measuring GHG

emissions from livestock as well as the range of methods that can be applied to reduce emissions, ranging from breeding to animal health and manure management. The collection also reviews nutritional approaches such as improving forage quality and the use of plant bioactive compounds and other feed supplements to limit emissions by modifying the rumen environment. Drawing in an international range of expert authors, Reducing greenhouse gas emissions from livestock production summarises what we can do to make livestock production more sustainable and viable for the future. It will be a major reference for the livestock (particularly dairy) science research community, environmental scientists, government and other agencies tackling the challenge of climate change, as well as companies involved in livestock production and processing of dairy and meat products. Key features A comprehensive review of both the causes of greenhouse gas emissions from livestock and the range of ways these emissions can be reduced Particularly strong focus on the range of nutritional strategies, from forage and silage to feed supplements such as plant bioactive compounds and direct-fed microbials as well as inhibitors and vaccines Covers other approaches such as genetics and selection, improved husbandry as well as manure management

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Reducing greenhouse gas emissions from livestock production

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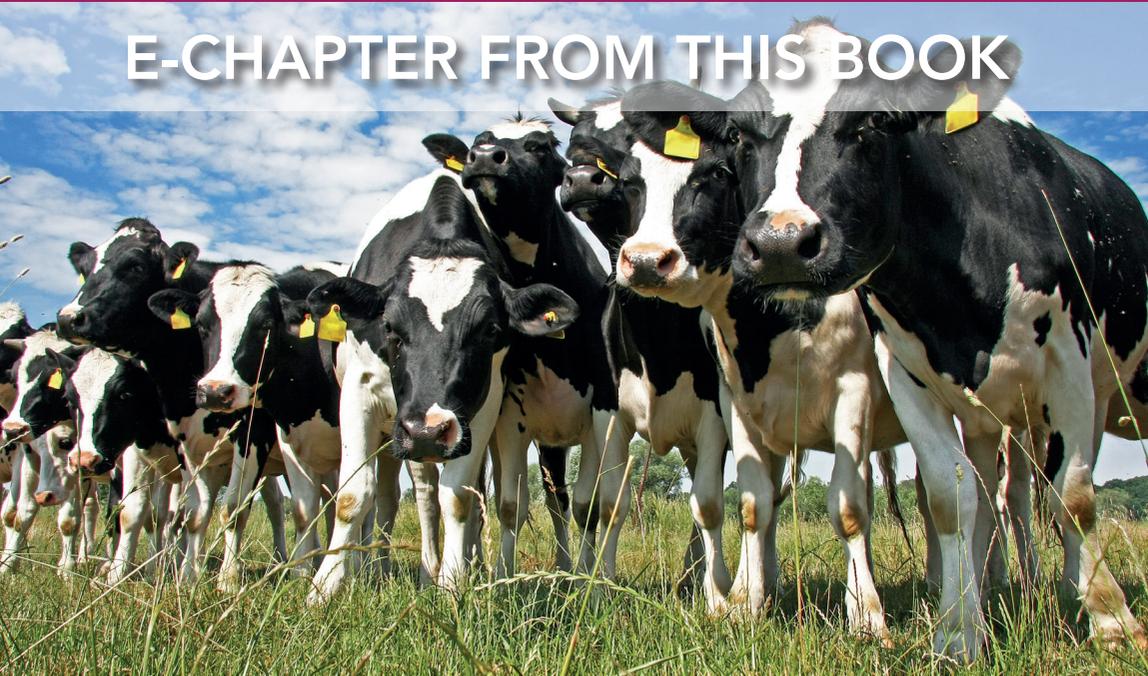
The impact of improving feed efficiency on the environmental impact of livestock production

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1 Introduction

As ruminants, cattle are marvellous bioreactors that, through symbiotic rumen fermentation, convert cellulosic plant biomass and other organic materials inedible to humans into high-quality animal proteins for human nutrition. Nevertheless, the conversion is of course not 100% efficient, and so varying quantities of waste products such as carbon dioxide (CO_2), methane (CH_4), and reactive nitrogenous compounds are emitted. As such, producers of ruminant livestock must strive to maximise output for each unit of input, both to enhance enterprise profitability and to minimise the environmental impacts of dairy and meat production. A key metric of this system efficiency is feed conversion efficiency (FCE), which for milk production is usually defined as energy-corrected

milk divided by feed dry matter intake (DMI) and for meat production is live weight gain divided by feed DMI. FCE per se also has a genetic component, which can be measured by residual feed intake (RFI). RFI is defined as the actual intake minus the feed intake expected to meet requirements for milk production, growth, reproduction and maintenance (Koch et al., 1963).

FCE has been widely used in beef production, as well as in pork and poultry production, to monitor the efficiency of feed utilization for growth. The dairy industry also recognizes the importance of the metric in management systems, but in addition to milk yield, there is also a need to account for body tissue loss and gain in calculating the efficiency of a lactating dairy cow (VandeHaar, 1998). Maximising the output of saleable product per unit of resource input is a standard principle of all manufacturing industries that relate directly to profitability. Another way of stating this relationship is that producers must minimise their unit cost of product and optimise their total unit output (Colman et al., 2011).

Relative to the reduction of greenhouse gases and contaminants of water, the simple concept is that the more carbon and nitrogen (N) in feedstuffs captured in the product, the less carbon and N are available for conversion into waste products (e.g. CO_2, CH_4 or urea N). By this principle, increasing milk or meat output from the same feed input requires changes in digestibility or postabsorptive nutrient metabolism with the result that less greenhouse gases and other waste products are produced per unit of milk or meat. The same principles apply to phosphorus and other nutrients that may become pollutants when they escape the animal through feaces or urine. This chapter will focus on the efficiency of milk production by dairy cattle related to nutrition and genetics focussing on how improving FCE can decrease the greenhouse gas burden of milk production and how FCE can be improved.

2 Greenhouse gases and dairy production

In the United States during 2008, the dairy sector's contribution to greenhouse gas emissions was estimated to be 134 Tg CO_2 equivalents, which equated to 1.9% of the total U.S. output (Thoma et al., 2013). Of this, CH_4, nitrous oxide (N_2O), and CO_2 contributed 44%, 13%, and 41%, respectively, of total emissions of the sector (Thoma et al., 2013). Emissions of CH_4 attributed to the dairy sector are primarily enteric emissions arising from digestive tract fermentation and stored manure, whereas N_2O emissions are largely attributable to N fertiliser application for the production of feedstuffs and manure application to farm land, including direct deposition by grazing livestock (Uweze et al., 2020; Rotz, 2018). In contrast, direct emissions of CO_2 arising from rumen fermentation and animal metabolism are not considered, as these emissions are a consequence of the digestion and metabolism of plant material incorporating atmospheric

CO_2 captured by photosynthesis. These estimates of the contribution of dairy production systems to global greenhouse gas emissions have been revisited recently because of the shorter half-life of CH_4 relative to CO_2. Methane from ruminants is also derived from the digestion of plant material, and over time CH_4 in the atmosphere is converted to CO_2, which reduces the long-term global warming effect of enteric CH_4 (Cain et al., 2019). In light of these considerations, dairy's contributions to CO_2 and N_2O emissions through fossil fuel consumption, fertilizer production and use, as well as manure management, are a greater concern for global warming in the longer term.

While the dairy sector is a small contributor relative to other industries such as oil and gas, the industry faces pressure to decrease greenhouse gas output. From the viewpoint of dairy producers, this pressure should not be viewed necessarily as burdensome because methane amounts to a 3.8–7.4% (5.6% on average) loss of gross energy intake from feeds (Kebreab et al., 2008). Mitigating greenhouse gas emissions should help not only the environment but also the financial bottom line of dairy production, unless the costs of mitigation become excessive. This is true especially if the feed energy not emitted as methane is captured as additional milk or body tissue (Reynolds et al., 2011). However, in most studies to date decreases in methane emission resulting from feeding methane inhibitory compounds such as 3-nitrooxypropanol (Reynolds et al., 2014; Hristov et al., 2015) or nitrate (Olijhoek et al., 2016) have not been associated with increases in milk energy yield or body energy balance. In this case, a part of the energy not emitted as methane is emitted as hydrogen, but the fate of the remainder of the methane energy not emitted is not certain (Olijhoek et al., 2016). In contrast, dietary strategies such as supplemental fat consistently decrease methane per kg feed DMI and often increase milk yield (Beauchemin and Grainger, 2011), but in this case, the effects on milk yield are through mechanisms independent from the effects on methane emission.

An issue with striving to decrease methane emissions is a decrease relative to what – in other words, what is the denominator of the equation? A reduction in total methane produced by the dairy sector will be difficult to achieve without reductions in animal numbers or effective mitigation strategies (e.g., methane-inhibiting feed supplements). Reductions in methane formation per unit of feed dry matter consumed (methane yield) may require shifts in the microbial community's overall metabolism or methanogenic enzyme inhibition through feed additives such as nitrate (Olijhoek et al., 2016) or 3-nitrooxypropanol (Hristov et al., 2015) as discussed above. Reductions in methane yield can also be achieved by feeding supplemental fat, which provides dietary energy that is not fermented in the rumen to yield hydrogen for methane synthesis (Grainger and Beauchemin, 2011). In contrast, decreases in methane production per unit of milk produced (methane intensity) are possible by boosting production efficiency (milk per unit of feed DMI). Much of this benefit arises from a dilution

of the greenhouse gas production associated with the maintenance intake of the animal (Knapp et al., 2014). Cows require a certain amount of feed nutrients to maintain critical life functions even in the absence of milk production; think of it as the 'overhead' digestion and metabolism needed to sustain the basic functions of cows. Increasing the amount of milk produced per unit of additional feed intake thus serves to dilute the amount of maintenance greenhouse gas production over a larger number of milk production units. Other ways that improving feed efficiency may decrease methane output per unit of milk produced relate to increasing rates of nutrient passage through the rumen, shifting site of digestion to the intestine, feeding supplemental fat, or reducing heat production by the animal by alterations in metabolism that result in greater milk yield (discussed in a later section).

3 Origin of methane and reactive nitrogen excretions

In ruminants, enteric methane is mostly produced by the reduction of CO_2 in the rumen and hindgut. Greenhouse gas (primarily methane) output by dairy cattle represents 24.2% of enteric emissions from livestock (USEPA, 2021). The majority of methane production (ca. 85%) occurs in the reticulorumen of cattle, with normally only 13% being produced in the lower gut and rectal emissions constituting only 2–3% of total animal emissions (Murray et al., 1976; Munoz et al., 2012). Thus, factors relating to feed quality, feed consumption, feed degradation, and ruminal metabolism are paramount for the determination of methane output by dairy cattle.

The rich and extensive microbiota in the rumen constantly degrades complex carbohydrates in the diet (cellulose, hemicellulose, pectin, and starch) and metabolizes the constituent monosaccharides to the principal short-chain or volatile fatty acids (VFA), which are acetate, propionate, and butyrate. Conversion of monosaccharides to VFA generates ATP that can be used to drive nucleic acid and protein biosynthesis, that is, the principal components of new microbial cells. Degradation of feed protein and nonprotein N, including urea N recycled to the rumen, provides substrates (NH_3, amino acids, peptides) for microbial amino acid and protein synthesis. Ammonia N not captured as microbial protein is absorbed, converted to urea N in the liver, and either recycled to the gastrointestinal tract or excreted in the urine. Urea recycled to the rumen and hindgut is degraded by microbial urease to CO_2 and NH_3, and the NH_3 is either used for microbial protein synthesis or is reabsorbed. Any microbial protein synthesized in the hindgut is excreted as faeces, and microbial protein can account for more than 50% of faecal non-ammonia N of lactating dairy cattle (Larsen et al., 2001). Urea N in urine is very reactive and can be quickly volatilised as NH_3, especially when urine is mixed with faeces containing microbial urease. Faecal protein N is less reactive than urinary

urea N, but as noted above, can contribute to N_2O and nitrate losses to the environment, depending on manure management practice.

Methane production serves a critical role within the microbial community. Production of acetate from fibre fermentation is associated with the co-production of CO_2 and H_2. The partial pressure of H_2 must be kept very low in the rumen to avoid poisoning the fermentation, and the primary means of doing so is the conversion of H_2 and CO_2 to CH_4 and H_2O (Hungate, 1966). The organisms responsible belong to the Archaea, but changes in Archaeal populations correlate only weakly with methane production (Tapio et al., 2017). Rather, methane production is related more to the populations of hydrogen-producing bacteria (Wallace et al., 2017). Production of propionate is not associated with the production of CO_2 or H_2; in fact, propionate uses hydrogen reducing equivalents in its synthesis. Although butyrate production also produces CO_2, it uses hydrogen reducing equivalents, so methane formation is not necessary (Hungate, 1966).

A fundamental relationship exists then in the fermentative breakdown of dietary components within the rumen, which can be appreciated by writing a simplified (non-chemically balanced) equation for rumen fermentation:

$$\text{dietary C and N} \rightarrow \text{microbial biomass} + \text{VFA} + CO_2 + CH_4 + H_2O + NH_3 + \text{heat} \quad (1)$$

From the standpoint of microbial growth efficiency, microbes strive to maximise biomass growth at a minimum VFA production, thus capturing as much of the starting feed substrate in new microbial cells as possible. The mixed rumen microbial population is able to generate 3–4 moles of ATP per mole of glucose fermented, which contrasts with simple monoculture fermentations that may generate only 2 moles of ATP (Hungate, 1966). Therefore, as rumen nutritionists, we understand that maximising microbial efficiency in the rumen ultimately leads to improved efficiency of milk production. Another way to think of this relationship is that the more dietary C and N we can keep in VFA and microbial protein, the less CH_4 and NO_2 are released into the environment. Similarly, the more efficiently dietary protein can be converted to milk protein through microbial protein synthesis and the metabolism of absorbed amino acids, the less excess N is excreted in urine and faeces. This idea forms the basis for why improving FCE decreases methane loss and the total greenhouse gas emissions attributable to dairy production.

4 Feed conversion efficiency

Improvements in milk production over the last several decades provide a clear demonstration of the benefits of improved FCE. Increases in FCE have arisen from increases in milk production, which dilutes the proportion of feed used for

maintenance (VandeHaar and St-Pierre, 2006). Milk production has increased from intense genetic selection, improved nutrition and cow health, and other advances in modern management techniques. The improved FCE has benefited dairy producers' profitability, decreased the environmental impact of milk production, reduced the amount of land required for milk production, and decreased the greenhouse gas emission per unit of milk produced (Knapp et al., 2014). Continued gains in FCE by these methods will diminish, however, because the effect diminishes with each increment of dilution of maintenance (VandeHaar, 1998; Reynolds et al., 2011; VandeHaar et al., 2016).

Many environmental factors also affect FCE, including nutrition. Diet digestibility, or more specifically forage digestibility, is a major component of FCE. Dietary protein and carbohydrate balance, supplemental fats and various additives may also impact FCE through effects on digestive function and milk energy yield. Other factors include the stage of lactation, body reserve changes, physical activity, mastitis or other diseases, acidosis and heat and cold stress. From a dairy system standpoint, the total FCE of the farm unit is impacted by numerous factors, including calving interval, days dry, age of first calving, reproductive efficiency, periparturient health disorders, and death loss in calves and heifers. These latter factors centre on the effects of decreased productive days of life for those animals that are not producing milk, or not producing large amounts of milk, but continue to consume the feed.

Herd and Arthur (2009) reviewed the biological basis for differences in RFI for beef cattle. Possible components included feed intake, digestion, metabolism associated with fat and protein deposition, physical activity, thermoregulation, and other components of basal metabolism. As reviewed by Reynolds et al. (2011), digestible energy is the most variable proportion of gross energy intake in ruminants. It accounted for 86% of the variation in dietary net energy for lactation in dairy cattle in the calorimetry studies on which the initial NEmilk system for energy requirements of lactating dairy cows in the USA was based (Moe et al., 1972). This largely reflects differences in forage quality and the digestibility of fibre, which is affected by forage maturity at harvest and processing during conservation and feeding, as well as associative effects of other diet components that impact the rate and extent of fibrolytic activity in the rumen.

Beever and Drackley (2013) calculated methane production per kilogram of milk production as a function of increasing milk production efficiency and found a negative relationship between the two (Fig. 1). That this theoretical calculation was borne out in practice was demonstrated by an analysis of 323 measurements of methane emission by lactating dairy cows at the University of Reading (Fig. 2). When expressed on the basis of MJ of methane emitted per MJ of milk energy production, there was a reduction in methane emission

Relationship between feed conversion efficiency (litre ECM per kg feed DM) and methane output expressed as grams/litre ECM
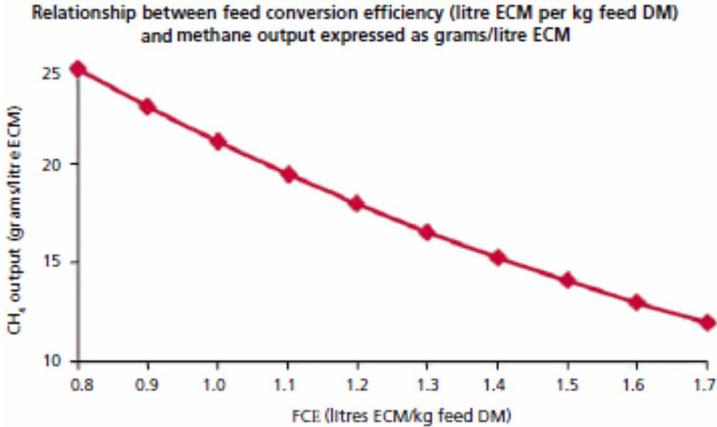
Figure 1 Theoretical relationship between methane output (g/L ECM) and FCE (L ECM/kg DM). Reprinted from Beever and Drackley (2013) with permission.
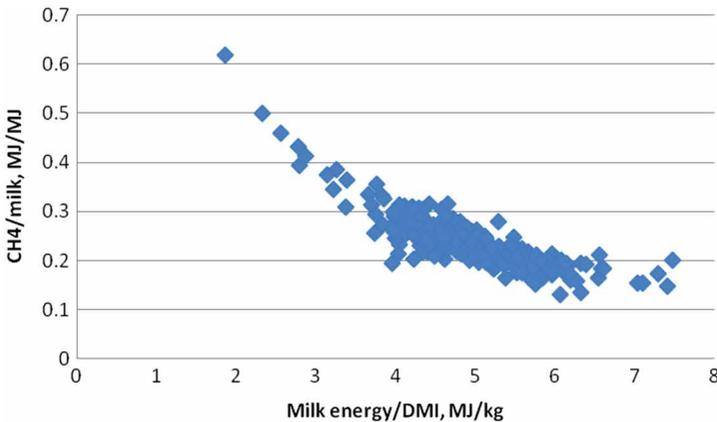

Figure 2 Methane energy/milk energy (MJ/day) as a function of milk energy (MJ/day) per unit feed dry matter intake (kg/day) where y = 0.833*exp$^{(-0.259*x)}$. Individual observations (n = 323) for cows fed various dietary treatments in experiments conducted at the University of Reading with correction for the random effect of experiment on the intercept.

per unit milk energy yield with increasing FCE, expressed as milk energy per kg feed DMI (MJ/kg). An exponential decay curve provided the best fit of the data after correction for the effect of experiment, clearly showing the higher methane 'overhead' of lower-yielding cows and the dilution of maintenance greenhouse gas 'costs' with higher milk yield and FCE. Similar relationships between increased milk yield per se and reduced methane emission per unit milk yield have been noted previously (Reynolds et al., 2011).

5 Nutritional practices to enhance feed conversion efficiency and decrease CH$_4$ excretion

Because methane formation occurs from microbial fermentation of dietary constituents, it follows that nutrition of the ruminant impacts FCE and methane production (Table 1). The most important aspect of nutrition is feed intake, represented in ruminants as DMI. A meta-analysis of methane measurements from growing and lactating cattle (Mills et al., 2009) revealed that feed DMI was the primary predictor of methane emission (Reynolds et al., 2011). The effect of DMI is explained by the increasing provision of fermentable substrates, although the use of digestible energy only marginally improved the prediction (Mills et al., 2009).

A commonly used equation to estimate methane production (Moe and Tyrrell, 1979) is as follows:

$$\begin{aligned} \text{methane production, MJ / d} = 1.837 + 1.142 \left(\text{digested soluble residue, kg/d}\right) \\ + 2.142 \left(\text{digested hemicellulose, kg/d}\right) \qquad (2) \\ + 5.828 \left(\text{digested cellulose, kg/d}\right). \end{aligned}$$

Since this early work of Moe and Tyrrell (1979), there have been numerous subsequent meta-analyses of measurements of methane emission relative to

Table 1 Feeding management variables and effects on methane (CH$_4$/ECM), dry matter intake (DMI), energy-corrected milk (ECM), and feed conversion efficiency (FCE). Modified from Knapp et al. (2014)

Feeding alteration	CH$_4$/ECM	DMI	ECM	FCE
Increased DMI	Decrease	Increase	Increase	Increase or no change
Increased forage quality	Decrease	Increase	Increase	Increase
Decreased forage particle size	No change	Increase	Increase or no change	No change
Grain processing	Decrease	No change	Increase or no change	Increase or no change
Increased concentrate feeding	Decrease	Increase	Increase	Increase or no change
Rumen pH <5.5	Decrease	No change or decrease	Decrease	Decrease
Brown midrib corn	Decrease	Increase	Increase	Increase or no change
Fat feeding	Decrease	Decrease or no change	Increase	Increase

diet intake and composition, which have largely confirmed the overriding role of intake of digestible structural and nonstructural carbohydrates, as well as lipids (see below), in determining methane emission and yield. For example, a recent global analysis of 3183 individual observations concluded that prediction models should include diet intake, digestibility, and concentrations of structural and nonstructural carbohydrates and ether extract for greatest accuracy (Benaouda et al., 2019).

According to Equation 2, increments of digested soluble residue, largely comprising starch and sugars, will increase methane to a lesser extent than digested hemicellulose or cellulose from forages. In turn, digested hemicellulose has a much smaller effect than digested cellulose. This is consistent with the fact that starch fermentation yields a greater proportion of propionate compared to fibre fermentation (Hungate, 1966). Increasing concentrate supplementation in the diet increases digestible energy, usually increases FCE, and decreases methane output per unit of milk produced, as predicted by the analysis in Fig. 2 and by the diluting effect of greater productivity on methane production per unit of milk yield. Concentrates containing cereal grains rich in starch will increase the metabolisable energy available to the animal, usually increasing milk yield unless excessive amounts are fed that cause acidosis (Van Soest, 1994).

In contrast, increasing the digestibility of forages, which will usually increase FCE by boosting milk yield, might not reliably change methane production per unit of milk produced because of the increase of fermented cellulose and hemicellulose. However, in practice, improving forage digestibility usually increases FCE and, by increasing milk production, the yield of methane per unit of ECM decreases due to the dilution of the maintenance concept. Variations in concentrations of cellulose, hemicellulose, and starch, as well as their digestibility, interact with differences in DMI that can make it difficult to predict the resulting methane production from differences in FCE (Reynolds et al., 2010; Livingstone et al., 2015). For example, diets higher in maize silage contained more starch and less NDF than diets higher in grass silage, and resulted in greater DMI and milk yields, but FCE was greater for the diets high in grass silage. However, methane intensity was greater for the high grass silage diets (Hammond et al., 2016).

Forage digestibility can be increased in several ways. Harvesting at younger maturity increases digestibility because of greater concentrations of nonstructural carbohydrates, such as sugars and fructans, along with lower lignification of plant cell walls (Van Soest, 1994). Some genetic variants have greater digestibility. For example, the stover from the *bm-3* or brown midrib genetic variant of maize and sorghum is more highly digested than typical varieties (Oba and Allen, 2000). Cellulose, hemicellulose, and NDF were less digestible in diets containing 40% (DM) maize silage and 10% alfalfa silage

than in diets containing 10% maize silage and 40% alfalfa silage (Ruppert et al., 2003). Finally, grass forage is typically more digestible than legumes, such as alfalfa, although the rate of fermentation is faster for legumes (Van Soest, 1994).

Processing forages can have contradictory effects on methane yield. Fine grinding or pelleting of forage increases the surface area available for fibrolytic microbiota to attach for fermentation, but the small particle size increases its passage from the rumen (Russell and Hespell, 1981), thus limiting the digested dry matter and so limiting methane formation (Moss et al., 2000). Such effects could decrease methane by 20–40% per unit of DM at high intakes, although at restricted intakes the effects are less (Johnson and Johnson, 1995). However, this also decreases potential energy delivery to the animal, which might decrease milk production, although compensatory hindgut digestion can recover some of the lost energy (Van Soest, 1994). With fine grinding of the forage and the resulting faster passage, however, the animal will likely eat more (Van Soest, 1994), which would tend to increase methane production.

Grains can be processed by grinding, rolling, and steam flaking, all of which increase surface area for digestion and decrease particle size. Grain processing can decrease the amount of starch that passes to the small intestine. Digestion in the small intestine should be more efficient energetically, but results have not borne this out in practice (Huntington et al., 2006). The effect of processing on ruminal degradation of starch varies among cereals and depends on the processing methods used (Svihus et al., 2005). Extensive rolling of barley maximised ruminal and postruminal digestion of starch (Yang et al., 2001). More extreme processing tends to increase total VFA concentration in the rumen, with a greater proportion of propionate that would decrease methane formation. Grinding maize grain increased starch digestibility in the total tract compared with rolling (Knowlton et al., 1998), but ground maize resulted in greater methane production (Wilkerson et al., 1997). Steam flaking maize grain resulted in greater FCE than grinding, regardless of particle size of grind (Ahmadi et al., 2020). However, finely ground maize can produce results similar to steam-flaked maize (Mathew et al., 2011). Heat treatment through pelleting, flaking, extruding, and toasting can change the ruminal degradation rates of protein and carbohydrates and decrease the acetate:propionate ratio in the rumen (Van Nevel and Demeyer, 1996). However, the relationship between such treatments and CH_4 emissions depends on the feed, composition of the total diet, and intake (Knapp et al., 2014).

Supplemental fats and oils are often added to diets for dairy cattle to increase the energy density of diets for high milk production (Palmquist and Jenkins, 2017). According to meta-analyses (Rabiee et al., 2012; Hu et al., 2017), fats usually maintain or decrease DMI while increasing milk yield and milk energy output. Consequently, supplemental fat sources often increase FCE and, as expected, decrease methane output per unit of milk energy (Ruppert

et al., 2003; Kliem et al., 2019). The effect of lipids on methane production is dependent on the source, fatty acid profile, inclusion rate, form of lipid, and diet composition (Beauchemin et al., 2008). Lipid sources replace fermentable substrates, and the unsaturated fatty acids provide an alternate sink for hydrogen disposal. Unsaturated fatty acids also directly impact fibre-fermenting microbiota and methanogens in the rumen (Czerkawski et al., 1966; Blaxter and Czerkawski, 1966). In practice, however, changes in methane production are not always observed. Nevertheless, a meta-analysis conducted by Knapp et al. (2014) found that increasing fat content of the diet decreased methane per unit of ECM, and that the type of lipid source affected the response. Free vegetable oils and endogenous lipids resulted in a greater reduction of methane per unit of ECM than did inert fats or seed lipids. Some seeds, vegetable oils, and medium-chain fatty acids (such as those found in coconut oil; Hristov et al., 2009) further decrease methane, but often at the expense of DMI, which could be detrimental to productivity and reproduction over the long term (Reynolds et al., 2011; Knapp et al., 2014).

In addition to 3-nitrooxypropanol and nitrate mentioned previously, a variety of potential nutritional additives have been tested for their ability to improve FCE and decrease methane losses, including ionophores, yeasts, certain seaweeds, and plant bioactive compounds with antimicrobial or digestive effects, such as tannins and essential oils (Beauchemin et al., 2008; McAllister and Newbold, 2008). These compounds have had varying efficacies, especially in the longer term, perhaps due to differences in dose rate and adaptation of the rumen microbes (Beauchemin et al., 2008). Although some have shown potential to decrease methane excretion, for these approaches to be widely adopted their effects will need to be consistent, sustained, without deleterious effects on feed intake, production, FCE or product quality, economic to adopt, and sustainable (Reynolds et al., 2011).

6 Nutritional practices to increase milk protein efficiency and decrease N_2O excretion

In ruminant production systems, enteric CH_4 production is the greatest contributor to greenhouse gas emissions, followed by CH_4 from manure and in beef feedlot systems, N_2O from pen surfaces, and N_2O emissions from soils (Montes et al., 2013). Improving the efficiency of dietary N use by increasing N incorporation into milk protein and decreasing N losses in faeces and urine will have positive effects on N_2O excretion and environmental contamination with N (Uwizeye et al., 2020). Many of the same principles discussed to this point relative to increasing FCE will have beneficial effects on increasing efficiency of dietary N use. From an environmental standpoint, animal practices to decrease urinary N loss have the biggest impact because urinary N is more susceptible

to leaching and volatile losses than faecal N and contributes directly to N_2O loss from livestock facility surfaces (Dijkstra et al., 2013a; Montes et al., 2013).

The main driver of N losses from cattle is N consumed in feed. Dairy cows secrete in milk an average of 21–33% of consumed N (Calsamiglia et al., 2010), with almost all the remaining N excreted in faeces and urine. In agreement, Reed et al. (2015) calculated an average total manure N excretion of 69% of N intake from a large database. Dijkstra et al. (2013b) calculated the theoretical upper limit of dietary N incorporation into milk protein to be 43% at maximal milk secretion for a cow weighing 650 kg and producing 40 kg/day of fat and protein corrected milk.

Huhtanen and Hristov (2009) concluded from a meta-analysis that dietary crude protein (CP) concentration is the most important dietary factor influencing milk N efficiency, with ruminal degradation of CP being of lesser importance. Differences in amount and, to a smaller extent, digestibility of N in feed affect not only the total amount excreted but also the partitioning of N among milk, urine, and faeces (Castillo et al., 2001; Kebreab et al., 2002). Partitioning of manure N excretion into faecal and urinary N excretion is important because differences in N intake largely affect urinary N output, which is of greater importance to reduce environmental impact (Dijkstra et al., 2013a).

The carbohydrate portion of the diet may impact the efficiency of dietary N use through differences in the amount or efficiency of N capture in the rumen. Ruminants must have sufficient ruminally degradable protein to maximise fermentation with the amount of fermentable carbohydrates supplied. Wilkinson and Garnsworthy (2017) showed that replacing dietary grazed grass or grass silage with corn silage at similar milk yield increased N efficiency and reduced the C footprint. Grazed grass is particularly problematic in terms of urinary N loss because of the high soluble CP content of the grass and concurrent lower content of rapidly fermentable carbohydrates (Hristov et al., 2013).

Dairy producers have often overfed dietary protein in the mistaken assumption that it would boost milk production (Broderick, 2018). Broderick (2003) compared diets with CP increasing from 15.1% to 16.7% and 18.4% by adding soya meal to the diet. Milk and milk protein yields increased with the first increment of CP but not the second. The only result from increasing dietary CP to 18.4% was the increased excretion of urinary N, which accounted for nearly all of the increment of dietary N. Recently, a trend for lower dietary CP has been observed in high-producing herds. Diets with as little as 14.9% CP can support milk production in excess of 45 kg/day when properly balanced for N and carbohydrate fractions and supplemented with key ruminally protected amino acids (Fessenden et al., 2020). In 2010, the five highest producing herds in the state of Wisconsin were being fed diets containing an average of 16.9% dietary CP, with the lowest at 16.3% (Broderick, 2018). Over the period from 2004 to 2010, CP content of dairy diets in Wisconsin decreased 1.1 percentage units,

but milk and protein production increased by 1700 and 51 kg per lactation. Clearly, minimising dietary CP needed to support high milk production pays dividends in the way of decreasing ration cost and environmental excretion of N, without sacrificing productivity.

7 Genetics and feed conversion efficiency

Using RFI as a measure of FCE has the advantage that it is independent of maintenance requirements and is not an efficiency determined by the level of production per se. A disadvantage of the measurement is that animals that are more efficient have negative RFI, which is non-intuitive and difficult for producers to accept. Reported heritability estimates of RFI in dairy cattle generally are low to moderate, with estimates ranging from 0.01 to 0.40 among lactating cows (Connor, 2015). Tempelman et al. (2015) determined that RFI had a heritability of 0.15–0.18. This means that the trait could be improved through genetic selection but that much of the variation in phenotype must be attributable to other environmental factors. Genetic correlations suggest no undesirable relationships detected between RFI and fat-corrected milk yield, productive life or feeding behaviours, and desirable relationships between RFI and predicted methane production in lactating cows (Connor, 2015).

There is currently interest in the potential selection of dairy cattle for improved feed efficiency (e.g. Lin et al., 2013; VandeHaar et al., 2020) and lower methane emission or methane yield (e.g. Breider et al., 2019; Lassen and Løvendahl, 2016). However, these traits must not be considered in isolation; for example, reductions in methane yield in sheep were shown to be driven by higher rates of feed passage through the rumen attributable to smaller rumen volume and thus reduced total feed intake capacity (Goopy et al., 2013).

The benefits of selection for RFI make the prospect of its application promising. For example, Holstein–Friesian heifers in New Zealand and Australia fed a forage-based diet that were in the bottom 10% of the sample population for RFI (i.e. most efficient) consumed 15%–20% less feed relative to heifers in the top 10% for RFI (least efficient; Williams et al., 2011; Waghorn et al., 2012). Differences are similar to differences in DMI of 12–13% reported in low versus high RFI groups of growing Angus–Hereford steers (Cruz et al., 2010). The dairy heifers cited showed no differences in feed intake, yields of milk or milk components, change in BW or body condition score when evaluated during days 75–195 of their first lactation (Macdonald et al., 2014). These results indicate that considerable savings in feed costs can be achieved by maintaining only the most feed-efficient growing heifers in the herd, with no negative consequences on future lactation performance.

In addition to selection for RFI, it might be possible to use genetic selection to improve N efficiency. Marshall et al. (2020) used breeding values for milk

urea N (MUN) to create high and low lines of Holstein–Friesian dairy cows. There was a positive relationship between MUN breeding value and MUN, with MUN decreasing 1.61 mg/dL per unit decrease in MUN breeding value. Urinary N concentration decreased 0.67 g/L per unit decrease of MUN breeding value, with no difference in urine volume or urinary frequency, which resulted in a 165 g/day decrease in urinary urea N excretion between animals with the highest and lowest MUN breeding value. At the same milk yield, milk protein percentage increased by 0.09 per unit of MUN breeding value. Such preliminary results are positive both for decreasing environmental excretion of N and for improving N partitioning into milk for greater producer profitability.

Relative to greenhouse gas emissions, cattle with lower RFI have a lower DMI than less efficient animals at similar production levels (Connor, 2015), thus decreasing one major contributor to CH_4 production. By definition, animals with lower RFI have less manure output for a given level of production, which should decrease the release of CH_4 and N_2O from stored manure (Montes et al., 2013). Recent research demonstrated that cows with greater FCE (lower RFI) also used protein more efficiently, which would help reduce N excretion in urine (Liu and VandeHaar, 2020).

8 Postabsorptive metabolism and feed conversion efficiency

Heat energy lost in the conversion of ME to net energy (NE) typically accounts for 20–30% of gross energy intake in dairy cattle. But, in contrast to digestibility, the variation and opportunities to decrease these losses are more limited. The effects of forage type, processing, and forage to concentrate ratio on the efficiency of ME utilisation for milk and meat production (and FCE) have been extensively researched (Reynolds, 2011). Such effects are a greater concern in extensive systems relying heavily on poorer quality forages. Because the digestive system and liver account for as much as 50% of body heat production in ruminants, their metabolism has an impact on the partial efficiency of ME use for production that is disproportionate to their mass. Forage amount and digestibility impact ME utilisation for NE, which is largely attributable to the tissues of the gut and may reflect differences in the work of digestion and gut mass (McLeod and Baldwin, 2000). In contrast, nutrient re-partitioning agents such as growth hormone impact energy utilisation by altering metabolism in the muscle, adipose tissue, and mammary gland to increase milk production, which improves FCE by dilution of maintenance.

Reducing losses of dietary energy as heat may be one of the main factors affected by selection for improved RFI. Only 19% of the variation in RFI among animals may be attributable to differences in diet digestion and heat of fermentation, with the remainder likely due to differences in physical activity,

body composition, protein turnover, and other metabolic processes associated with maintenance requirements and partitioning of nutrients between protein and lipid deposition (Herd and Arthur, 2009).

The effects of excess protein on energy utilisation in cattle have generated much discussion. Tyrrell et al. (1970) reviewed results of calorimetry studies and reported a reduction in ME or NE of diets when digestible protein was fed in excess of requirements. This effect was included in the calculation of NE for lactation (Moe et al., 1972). Some have attributed this effect of excess protein to the energy costs of urea synthesis in the liver, but studies in sheep and cattle catheterised for measurements of liver metabolism have consistently failed to show an effect of increased ammonia absorption and subsequent urea production by the liver on hepatic oxygen consumption (Reynolds, 2006). In contrast, supplemental protein fed in excess of requirement does increase liver oxygen use (i.e. heat production), as well as oxygen use by the gut, suggesting that the effect of excess protein on the efficiency of energy utilisation is associated with amino acid catabolism, rather than urea synthesis per se (Reynolds, 2006). Over 100 years ago, Rubner showed that the postprandial rise in heat production in dogs, termed 'specific dynamic action', associated with consumption of protein was greater than for carbohydrates and fats (Brody, 1939), which also reflects the catabolism of amino acids in excess of requirements. These effects might be attributable to stimulation of protein turnover and greater activation of the sympathetic nervous system. Regardless of the mechanism, the potential benefits of feeding protein and ruminally protected amino acids more precisely to cattle extend beyond just the environment and economics to improving FCE.

9 Conclusion

Methane intensity of dairy production is related inversely to FCE. By diluting methane associated with cow maintenance, increasing milk production and increased FCE serve to decrease methane production per unit of milk energy produced. Nutritional practices that boost productivity usually boost FCE and will help to decrease methane intensity. Some of these include improving forage quality, increasing concentrate supplementation, and using supplemental fats and oils. Genetic selection for improved FCE (measured by RFI) will decrease methane intensity. Minimising dietary CP will help decrease urinary N losses, which contribute to increased N_2O and decreased efficiency of N capture into milk protein.

10 Future trends in research

Increasing FCE is directly related to profitability and will be a continued goal of research for improvement in the dairy industry. Decreased methane intensity

should be a collateral benefit of such improvement. Determining the genetic basis for FCE, as measured by RFI, may eventually lead to improvements in the overall efficiency of milk production. Improving genetic aspects of forage digestibility and methods to improve use by cows will help decrease methane intensity. The research will continue to find compounds or strategies that will decrease methane yield without compromising DMI or productive efficiency. Novel mitigation strategies might include inhibitors or early life microbial modulation to change the balance between hydrogen producers and methanogens. In addition, the possibility that synergistic effects between strategies might occur, such as combining 3-nitrooxypropanol with lipids, should be investigated. Research will continue to identify genetic opportunities to minimise the environmental burden of livestock production as well as urinary N excretion.

11 Where to look for further information

A comprehensive discussion of strategies to mitigate methane emissions in dairy cattle can be found in Knapp, J. R., Laur, G. L., Vadas, P. A., Weiss, W. P., and Tricarico, J. M. (2014), 'Invited review: Enteric methane in dairy cattle production: Quantifying the opportunities and impact of reducing emissions', *J. Dairy Sci.,* 97, 3231–3261.

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