Title:

Methodologies to quantify gas production and variance components associated with gas production from beef cattle

Author:

Elizabeth Dressler

Biographical sketch (please do not exceed 250 words):

Elizabeth Dressler was raised on a small cow-calf operation in Berryton KS. She received her bachelor's degree in Animal Sciences and Industry from Kansas State University in 2020. She completed her master's degree in Animal Breeding and Genetics at Kansas State University in 2022 where her research focus was on the sustainability of the beef industry and methane emissions from grazing beef cattle. Elizabeth is currently working on a Ph.D. at Kansas State University under Dr. Megan Rolf where she is continuing her research on methane emissions from beef cattle as well as completing a genetic evaluation of cashmere fiber production.

Advisor Name:

Dr. Megan Rolf

Advisor Approval:

I certify that I have read and had sufficient time to provide feedback on the attached literature review.

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Introduction

Methane (CH_4) is the second most abundant anthropogenic greenhouse gas (GHG) after carbon dioxide (U.S. EPA, 2021). In the United States, 27.1% of CH_4 emissions come from enteric fermentation of livestock species (U.S. EPA, 2021). Ruminant livestock species such as cattle, buffalo, sheep, and goats emit CH_4 as part of their natural digestive process.

The sustainability of the beef industry is a popular topic in news and social media. In the beef industry, CH_4 production effects all three pillars of sustainability: environmental protection, social equity, and economic viability. Atmospheric CH_4 absorbs and emits radiant energy; this traps heat in the atmosphere and is why CH_4 is considered a greenhouse gas (U.S. EPA, 2021). Social sustainability includes community and organizational resilience. Methane is related to global warming which can disrupt the livelihoods of people by making the environment and activities within it less resilient (U.S. EPA, 2021). More broadly, CH_4 production is tied to the impact beef production has on the viability, economy, and employment of rural communities. Economically, CH_4 production from enteric fermentation in beef cattle represents a decrease in efficiency for cattle production. Ruminants lose 5.5% to 6.5% of gross feed intake to enteric CH_4 production (Johnson & Ward, 1996). Thus, methanogenesis not only creates a greenhouse gas but is an energetically wasteful process. While CH_4 production from ruminants may never be zero, a portion of the estimated 5.5% to 6.5% of gross energy lost instead could have been used by the animal for a metabolically productive process. Since methanogenesis is a part of the biological process that allows ruminants to upcycle forage, maintaining animal productivity while mitigating greenhouse gas emissions is crucial.

Review of Literature

Enteric Methane Production

Methane is a gas that is produced through ruminant fermentation as a part of their normal digestive processes. Microbes within the rumen work synergistically to convert human indigestible plants into short chain fatty acids and proteins (Janssen, 2010). The main products of fermentation are volatile fatty acids (VFAs) such as acetate, propionate, and butyrate (Janssen, 2010). The short chain fatty acids are primarily absorbed across the rumen wall and provide the animal with energy which allow the animal to maintain homeostasis, reproduce, lactate, and grow. However, by-products are produced from the fermentation process such as hydrogen,

ammonia, and carbon dioxide (Janssen, 2010). Methanogenic archaea in the rumen use fermentation by-products to produce methane (McGovern et al., 2020). Hydrogen produced from the fermentation process is utilized as an energy source by methanogens to reduce CO_2 to CH_4 (Hunerberg et al., 2015). Methanogens have an important digestive function in the rumen because they are responsible for removal of H_2, which otherwise could accumulate in the rumen and have an inhibitory effect on fermentation rate and microbial function (Van Kessel and Russell, 1996; McAllister and Newbold, 2008).

Ruminants produce methane through fermentation in both the rumen and hindgut. According to Murray et al. (1975), 87% of methane is produced in the rumen and 13% is produced in the hindgut. Methane is released from the animal three different ways: 1) methane produced in the rumen and hindgut is absorbed in the blood and released by expiration through the lungs, 2) methane is directly released by eructation, 3) methane is released from the hindgut in flatus (Murray et. al., 1975). Of the methane produced in the hindgut, 89% (11% of the total CH_4 produced) is absorbed into the blood and released through expiration. Only 1-3% of total methane produced is released by flatus (Murray et al., 1975, Muñoz et al., 2012). The methane produced in the rumen is dispersed primarily by eructation and a small amount expiration through the lungs. Most methods to quantify gas emissions exclude the small percentage of CH_4 released in flatus and only quantify CH_4 eructated and expired.

Methods to Quantify Enteric Methane Production

Several strategies to mitigate methane emissions have been researched related to diet such as supplementation with fats (McGinn et al., 2004), ionophores (Appuhamy et al., 2013), probiotics (Ghorbani et al., 2002), nitrate (Nolan et al., 2010) and others. However, genetic selection is a mitigation strategy that would result in permanent and cumulative change. Large scale research to accurately quantify enteric methane production phenotypes is crucial for genetic evaluation. There are several methods to quantify CH_4 production from cattle including prediction models, respiration chambers, the sulfur-hexafluoride tracer technique, infrared spectroscopy, and open-circuit gas quantification systems. Each method has distinct advantages and disadvantages for phenotype data collection to be used in genetic evaluations.

Prediction Models. Prediction models can be used to predict CH_4 emissions rather than directly measuring emissions from animals using a quantification technique. A vast number of prediction models have been published with a range of different data inputs from DMI to milk production characteristics (Dijkstra et al., 2011; van Engelen et al., 2015, Uemoto et al., 2020; Mills et al., 2003; Moe and Tyrrell, 1979; IPCC, 2006).

Measuring CH_4 production is often expensive and requires complex equipment. However, an advantage to prediction models is that additional equipment is not required to estimate CH_4 production (Kebreab et al., 2016). In addition, empirical prediction models are relatively simple and require fewer input variables than mechanistic models (Appuhamy et al., 2016). However, there are several drawbacks to prediction models. The predictive power of the model depends upon the accuracy of the mathematical equation and the data inputs used in that equation (Kebreab et al., 2016). Errors in estimating feed intake, stoichiometry of volatile fatty acids, and rumen fermentation conditions were identified by Bannink et al. (2011) as the most likely sources of uncertainty in mechanistic models. Another disadvantage of prediction models is that the model assumptions may not be met in all situations, especially commercial livestock operations (Kebreab et al., 2016). For example, one assumption is that animals are healthy and not affected by environmental conditions, although this scenario is rarely true of all animals.

One of the biggest drawbacks to prediction models is that prediction models do not provide individual animal estimates distinct from differences in feed intake (Lakamp et al., 2022). Therefore, there is no opportunity to identify and select animals which have lower CH_4 emissions than other animals at the same feed intake amount, which would be critical for genetic evaluation. Prediction models are probably best applied to efforts to estimate CH_4 production from large groups of animals where mean production and feed intake are likely to be accurate for the entire group. In general, prediction models can be useful, especially if all necessary variables are readily available or quantification equipment is not available. But prediction models are less useful for the prediction of CH_4 from individual animals, such as necessary for genetic evaluation, for which a gas quantification technology would be preferred.

Respiration Chambers. Respiration chambers are considered the gold standard for CH_4 emission quantification, though every system has its strengths and weaknesses. Respiration chambers are a whole-animal open-circuit “room” used to measure respiratory exchange and gas fluxes.

Inflowing air is circulated in the chamber and mixed with emitted gases. The amount of gas emitted is found by comparing the concentration of that gas in the inflowing and outflowing air (Hammond et al., 2016). One advantage of respiration chambers is that both ruminal and hindgut CH_4 emissions are captured. Respiration chambers capture the estimated 1-3% of emissions in flatus (Murray et al., 1975; Muñoz et al., 2012), whereas other techniques don't capture hindgut CH_4.

Respiration chambers require the animal to be pulled from their normal environment and housed individually which can cause changes in animal behavior and lower dry matter intake (DMI). For example, in a study done by McGinn et al. (2004), steers were moved from their normal pens outside into respiration chambers, resulting in a decrease in DMI of 15% to 19%. Sheep in respiration chambers have 15% to 25% lower feed intake compared to their feed intake the previous week in individual indoor home pens (Bickell et al., 2014). The decrease in DMI associated with respiration chambers is likely due to the stress of handling and their new environment. Animals using a respiration chamber can experience stress from relocation and feeding pattern disruption. A lower DMI leads to an underestimation of methane emission, which may be the most severe in the most stressed animals- confounding two different traits. Therefore, the methane production observed in a respiration chamber can be lower than the actual production in the animal's normal environment, resulting in an underestimation of methane production of individuals and more broadly if used in a life cycle assessment, for example.

Additionally, respiration chambers are expensive to construct and maintain, and extensive labor is required for animal training and care (Johnson & Johnson, 1995; Arthur et al., 2017). These factors often limit the number of animals that can be measured. A sufficient sample size is imperative for genetic improvement studies, so these systems pose a major limitation to that work. Studies that use respiration chambers generally have high quality data, provided gas recovery tests are satisfactory, but require more time and resources to obtain a sufficient sample size compared to other techniques.

Sulfur-hexafluoride tracer technique. The sulfur-hexafluoride (SF_6) tracer technique was one of the first techniques developed to measure gas emissions in an open-air environment without confinement (Zimmerman, 1993). An inert bolus containing liquid SF_6 is placed in the rumen of the animal. The SF_6 is slowly released from the bolus in gaseous form through permeations in the

bolus at a known rate. The animal wears a halter with a capillary tube that is connected to an evacuated sample container on its back or an inflatable neck collar. The vacuum in the sampling container collects the metabolic and tracer gas from the nose and mouth. After the trial, CH_4 and SF_6 concentrations are determined using the known permeation rate of SF_6 from the bolus and the mixing ratio of gases collected in the sampling container (Zimmerman, 1993).

The advantage of the SF_6 tracer technique is that animals are not restrained or enclosed in a chamber (Gunter and Beck, 2018). Although, there are several disadvantages of the SF_6 tracer technique. The SF_6 tracer technique does not account for CH_4 released as rectal flatus (Gunter and Beck, 2018; Murray et al., 1975). Another disadvantage is that extensive labor is required. The animals must be trained to wear the halter and the sampling container, which is laborious (Gunter and Beck, 2018). In addition, labor is required to insert the bolus into the animal's rumen. For these reasons, this technique is typically only used in short duration with a small number of animals, which limits possible applications for genetic improvement.

Infrared spectroscopy. Infrared spectroscopy is a method to measure CH_4 primarily used in dairy cattle. One type, Fourier transform infrared (FTIR), uses infrared transmission spectrum to identify an absorbance spectrum from an air sample (Teye et al., 2009). Then gas densities can be calculated for each sample using the absorbance spectrum. Another infrared spectroscopy method of gas quantification is based on mid-infrared spectra. Infrared spectroscopy methods have the advantage that they are non-invasive, and animals can remain in normal production environments during collection. However, measurements are highly variable and require several hundred measurements during a short period of time to quantify individual animal means (Lassen & Løvendahl, 2015). This is one reason why this method is primarily only used for dairy cows, because the data can be collected during times of feeding or milking.

Open-circuit gas quantification systems. An open-circuit gas quantification system (OCGQS) is an automated technology that quantifies gas fluxes by exhausting air past an animal's head and into the system while the animal is eating a small amount of bait feed (Hristov et al., 2015). The GreenFeed system (C-Lock, Inc., Rapid City, South Dakota) is currently the only OCGQS product on the market for commercial use. The OCGQS entices animals to visit the unit multiple times a day by releasing a small amount of pelleted feed as bait. Individual animals insert their

head into the hood and the OCGQS measures gas fluxes as air is continuously drawn past the head of the animal. The OCGQS collects several short-term breath samples throughout the day to calculate gas production rates (Herd et al., 2020). Measurements are an accumulation of spot samples, unlike the continuous sampling of respiration chambers and the SF_6 technique.

One of the main advantages of the OCGQS is that data can be collected on grazing animals in a pasture setting. It is ideal for CH_4 emissions of grazing animals to be measured during grazing so that estimates are representative of diet and grazing behavior (Waghorn et al., 2016). Another advantage of the OCGQS is that animals are unencumbered by respiration equipment or respiration chambers and do not require extensive training.

A disadvantage of the OCGQS system is that spot samples throughout the day are combined to calculate the daily CH_4 production, as detailed in Huhtanen et al. (2015). One concern with the OCGQS is if the spot samples throughout the day capture the variation in CH_4 emissions due to circadian rhythms. Hammond et al. (2016) recommended that a sufficient number of samples and with adequate sample length is included in the sampling protocol to account for diurnal variation of emissions.

Phenotypic Methane Production Traits

After CH_4 is quantified by one of the various methodologies, several CH_4 phenotypic traits can be calculated (Table 1). Individual animal CH_4 production expressed on a daily basis is referred to as methane production or methane production rate (MPR) which is simply the amount of CH_4 produced by an animal per day. In an effort to account for animal productivity, other phenotypic ratio traits have been developed. Methane yield (MY) is the ratio of CH_4 (g) over a unit of feed intake, usually DMI (kg). Methane intensity (MI) is the ratio of CH_4 (g) over a unit of animal product. In beef cattle, MI is typically expressed over a weight measurement while for dairy cattle, MI typically includes a milk production trait. Additionally, several residual methane phenotypes have been developed. Residual methane production (RMP) is the actual MPR minus the expected MPR. The difficulty with RMP is calculating expected MPR which is commonly done using published regression equations usually including DMI (Blaxter and Clapperton, 1965; Johnson et al., 1995; IPCC, 2006; Kennedy et al., 1993; Dijkstra et al., 2011; de Haas et al., 2011).

Genetic Parameters

All CH_4 quantification methodologies discussed could be used to collect phenotypes for genetic evaluation. While some methodologies have distinct advantages, they all have challenges of phenotype collection for the purposes of genetic evaluation. Collection of a sufficient number of phenotypes for genetic evaluation is expensive, time-consuming, laborious, and requires proper contemporary grouping. Therefore, estimates of heritability and genetic parameters for CH_4 production in literature are fairly sparse for beef cattle (Table 2).

Hayes et al. (2016) derived genomic estimated breeding values (GEBV) for CH_4 traits from a reference set of 747 Angus cattle with a validation set on 273 additional Angus cattle. All animals in this study were born and raised on pasture, except for the period of CH_4 measurement where they were fed a roughage diet consisting of alfalfa and oaten hay chaff in the respiration chamber. Methane production rate, MY, and four RMP traits were measured in respiration chambers. The estimated genomic heritability derived from only genomic information for MPR was 0.28 ± 0.06 and 0.20 ± 0.05 for MY (Hayes et al., 2016). Hayes et al. (2016) reported moderate accuracies of GEBV calculated from genomic BLUP for MPR and MY (0.32 ± 0.04 and 0.37 ± 0.09, respectively).

Manzanilla-Pech et al. (2016) estimated heritabilities for a variety of CH_4 traits on 1,020 Angus beef cattle (partially the same animals as Hayes et al. 2016) collected utilizing respiration chambers and in two validation populations of Holstein dairy cows collected with the SF_6 tracer technique. The CH_4 traits evaluated for the Angus population were MPR, MY, MI, residual phenotypic methane (RPM), and residual genetic methane (RGM). Residual phenotypic methane and RGM were calculated based on the residual phenotypic and genetic regressions of a trivariate analysis of MPR, DMI and weight. The estimated heritabilities for MPR, MY, MI, RPM, and RGM in the Angus population were 0.30 ± 0.06, 0.20 ± 0.05, 0.25 ± 0.06, 0.19 ± 0.05, and 0.15 ± 0.05, respectively (Manzanilla-Pech et al., 2016). Heritabilities for the Holstein population were only evaluated for 3 CH_4 traits and different values were found. The estimated heritabilities for MPR, MY, and MI were 0.23, 0.30, and 0.42, respectively (Manzanilla-Pech et al., 2016). It is unknown whether the difference in heritability estimates was due to genetics or the smaller population size and higher associated standard errors (approximately 0.23). The authors concluded that CH_4 is a moderately heritable trait, and several factors need to be evaluated to determine which trait is the "best" measure of CH_4 emissions.

Donoghue et al. (2016) found genetic and phenotypic variance and covariance estimates for CH_4 emission traits. Using largely the same animals as Manzanilla-Pech et al. (2016) and Hayes et al. (2016), this study included data on Angus 1,046 animals that were born and raised on pasture. Methane emissions were measured in a respiration chamber for two days while animals ate a roughage-based diet. The traits evaluated were MPR, MY and 4 residual methane production traits as well as production traits such as birth weight (BW), weaning weight (WW), yearling weight (YW), final weight (FW). Carcass traits such as ultrasound measures of eye muscle area (EMA), rump fat depth, rib fat depth, and intramuscular fat were also included. One objective of this study was to estimate phenotypic and genetic correlations between the CH_4 and production traits (Donoghue et al., 2016). Donoghue et al. (2016) estimated the heritability of MPR and MY to be 0.27 ± 0.07 and 0.22 ± 0.06, respectively. All four forms of RMP had an estimated heritability of 0.19. Methane production rate and MY had a phenotypic correlation of 0.68 ± 0.02; this indicates that animals with high MPR also have high MY. Donoghue et al. (2016) hypothesized that reducing MY will not impact DMI because the two traits are not genetically correlated (-0.04 ± 0.18), however reducing MY will have a correlated effect on MPR because the two traits have a strong genetic correlation (0.50 ± 0.14). Interestingly, Donoghue et al. (2016) found that MPR had a weaker phenotypic correlation with BW (0.26 ± 0.04) than later in life growth traits such as WW (0.53 ± 0.03), YW (0.61 ± 0.03), and FW (0.56 ± 0.03). Genetic correlations between MPR and production traits were moderate to strong: BW (0.36 ± 0.18), EMA (0.40 ± 0.16), WW (0.84 ± 0.09), YW (0.86 ± 0.06), and FW (0.79 ± 0.08; Donoghue et al., 2016). Donoghue et al. (2016) speculated that the strong genetic correlations between MPR and animal weight traits is likely due to the strong association between MPR and DMI. This means that reducing MPR will have a correlated reduction in animal weight for the progeny. Instead, the authors proposed the mitigation strategy of selecting for reduced MY or residual methane because it should reduce CH_4 production without a negative effect on DMI (Donoghue et al., 2016).

Although dairy cattle are different from beef cattle in many ways, heritability estimates from dairy cattle can give insight into beef cattle. Three CH_4 phenotypes including CH_4:CO_2 ratio, CH_4 production (g/d) measured over a week, and CH_4 intensity (g CH_4/L milk produced), were measured for 3,121 Holstein dairy cows using an automatic milking system and FTIF detection (Lassen & Løvendahl, 2015). Both CH_4 production and CH_4 intensity had heritabilities

of 0.21 ± 0.06 and CH_4:CO_2 ratio had a heritability of 0.16 ± 0.04 (Lassen & Løvendahl, 2015). Methane production and CH_4:CO_2 ratio had strong genetic correlations to fat- and protein-corrected milk yield, (0.43 ± 0.10 and 0.37 ± 0.07 respectively; Lassen & Løvendahl, 2015). These estimates suggest that CH_4 production in dairy cattle is a heritable trait and that a strong genetic potential for milk production could be related to greater CH_4 emissions.

van Engelen et al. (2015) used milk composition information (milk fatty acid profile) in three different MY prediction equations to estimate MY of 1,905 Holstein-Friesian cows. The heritability estimates from the three different equations for CH_4 yield were 0.12 ± 0.06, 0.20 ± 0.07, and 0.44 ± 0.10 (van Engelen et al., 2015), suggesting methane yield based on milk fat composition is heritable.

Pickering et al. (2015) used feed intake, milk yield, live weight, and body condition scores to predict CH_4 emissions of 1,726 dairy cows. Predicted methane emissions (PME) was calculated daily from morning and evening milkings then averaged for each week of lactation. PME (g/d) had a mean heritability of 0.13 ± 0.04 across 44 weeks of lactation (Pickering et al., 2015). The heritability of PME stayed relatively stable across the 44 weeks of lactation measured. Pickering et al. (2015) also used a laser CH_4 detector to obtain repeated measurements from 57 cows. The repeatability of emissions from the laser CH_4 detector within lactation was 0.07 ± 0.08 and across lactations was 0.03 ± 0.08. The authors speculated that the low repeatability associated with the laser CH_4 detector was associated with the small sample size. Therefore, the laser CH_4 detector was found to not be suitable for genetic prediction due to low repeatability and difficulty in obtaining a sufficient sample size (Pickering et al., 2015).

Methane emissions were predicted from feed intake, milk and body weight data on 548 Holstein-Friesian heifers (de Haas et al., 2011). Predicted CH_4 emissions gradually increased throughout lactation until it reached a plateau around 400 g/d in mid-lactation until the end of lactation (de Haas et al., 2011). de Haas et al. (2011) estimated that PME had a heritability of 0.35 ± 0.12 for week 0 through week 42 of lactation. Heritabilities estimates varied between weeks of lactation from 0.29 to 0.42 with standard errors ranging from 0.10 to 0.12 (de Haas et al., 2011). Feed intake data collected from automated feeders was used to calculate RFI and DMI. Predicted CH_4 emissions had a strong positive phenotypic correlation with RFI, indicating that animals with lower RFI also would have lower PME (de Haas et al., 2011).

Kandel et al. (2017) studied two milk mid-infrared based CH_4 proxies: PME and log-transformed CH_4 intensity (LMI). The fatty acid profile was predicted using mid-infrared spectrometry and then an equation developed by Vanlierde et al. (2015) was used to find PME given the mid-infrared milk information (Kandel et al., 2017). Log-transformed CH_4 intensity was found by log-transforming the ratio of PME over daily methane yield. Kandel et al. (2017) studied both first (n = 56,957) and second (n = 34,992) parity cows. The heritability of PME was moderate and slightly decreased from first to second lactation, 0.25 ± 0.01 and 0.22 ± 0.01, respectively (Kandel et al., 2017). The heritability of LMI was 0.18 ± 0.01 for first lactation and 0.17 ±0.02 for second lactation (Kandel et al., 2017). Between first and second lactation, PME increased (433 g/d vs. 453g/d) while LMI decreased (2.93 vs. 2.86; Kandel et al., 2017). The authors suggested that the rankings of animals were similar between the two lactations based on the high Spearman correlation values for PME and LMI, 0.92 and 0.95 respectively (Kandel et al., 2017). Kandel et al. (2017) explained that the differences in values observed between first and second lactation were due to changes in feed intake, feed efficiency, energy partitioning, and milk production. Although PME is lowly heritable, it is a problematic trait to use for genetic selection. Predicted methane is calculated using various component traits, therefore those component traits change with selection rather than directly selecting for CH_4.

Although a different species, sheep are grazing ruminant animals that also produce CH_4. Sheep are typically less expensive to manage and are easier to handle, offering a potential proxy for cattle in CH_4 emissions research. Robinson et al. (2010) evaluated 708 grazing ewes for 1-hour CH_4 emissions using a sealed polycarbonate booth. The heritability of 1-hour CH_4 production (dL/hour) after adjustments for live weight was 0.13 with a repeatability of 0.32 (Robinson et al., 2010).

Pinares-Patiño et al. (2013) measured MPR and MY from 1225 sheep in respiration chambers. The heritability of MPR and MY was 0.29 ± 0.05 and 0.13 ± 0.03, respectively (Pinares-Patiño et al., 2013). Measurements in respiration chambers were repeated 14 days later to assess repeatability. Methane production and MY had repeatabilities of 0.55 ± 0.02 and 0.26 ± 0.02, respectively (Pinares-Patiño et al., 2013). The results of this study indicate that CH_4 emission traits are heritable and repeatable for sheep.

Conclusions and Implications to Genetic Improvement of Beef Cattle

Methane is a potent greenhouse gas with adverse effects on the environment due to the warming potential of the atmosphere (U.S. EPA. 2021). Enteric fermentation from ruminant animals is a source of CH_4 production and represents an energetic loss for that animal (Johnson & Ward., 1996). Several methods exist to quantify CH_4 emissions from cattle, including respiration calorimetry, the sulfur-hexafluoride tracer technique, prediction models, infrared spectroscopy and OCGQS. Each of the methodologies have advantages and disadvantages and some methodologies are better suited for collecting phenotypes for genetic evaluation than others.

The goal is to reduce CH_4 emissions from beef cattle to optimize productivity and profitability with sustainability. However, CH_4 production is a natural ruminant digestive process that allows cattle to digest and ferment human non-edible plant material. Therefore, it is vital that selection strategies incorporate the optimum balance between CH_4 production and animal productivity, as maximum productivity and minimum emissions are likely incompatible.

High feed intake is associated with high MPR in ruminants (Blaxter & Clapperton, 1965). Production traits such as growth are highly correlated with feed intake (Arthur et al., 2001). Therefore, reducing MPR could have an unfavorable impact on animal productivity due to the correlation with feed intake. Herd et al. (2014) evaluated several ways to measure CH_4 including MPR, MY, and four forms of RMP. Herd et al. (2014) estimated the phenotypic relationships between the CH_4 traits and the production traits. MPR was positively correlated with DMI, MY, RMP, growth traits, and body composition traits (0.65 ± 0.02; 0.72 ± 0.02; 0.65 to 0.79; 0.19 to 0.57; 0.13 to 0.29). However, MY was not correlated with DMI, growth traits, or body composition traits (-0.02 ± 0.04; -.03 to 0.11; 0.01 to 0.06). All four forms of RMP were strongly correlated with MY (0.82 to 0.95; Herd et al. 2014). These results suggest that reducing MPR as a mitigation strategy would have a negative impact on growth and body composition traits. However, MY was not correlated with DMI, but was positively correlated with MPR. This indicates that reducing MY would have no effect on DMI or animal productivity but would have a correlated reducing effect on MPR. Considering the undesirability of a ratio trait for genetic evaluation, one of the RMP traits could be used instead of MY. Additionally, an RMP trait independent from DMI may be the best trait to incorporate into selection strategies (Herd et al. 2014). The correlations from Herd et al. (2014) are phenotypic correlations therefore, future

research on the genetic relationships between these traits and growth traits is needed to decide which CH_4 trait should be incorporated into selection strategies.

Development of a selection index for CH_4 production may be the most advantageous mitigation strategy. A well-constructed index with properly weighted traits would allow for optimum selection to reduce CH_4 production without compromising important production traits, such as DMI. One of the biggest difficulties of selection indexes is assigning the appropriate economic weighting to each trait in the index. Currently, the economic value of enteric CH_4 emissions is unknown and the price of carbon is not globally realized (Lakamp et al., 2022). Further research is required in this area to define economic values for CH_4 production and evaluate its weighting in a selection index. Additionally, continued CH_4 phenotype data collection is needed for large-scale genetic evaluations to establish genetic correlations between CH_4 production and other economically important traits (LaKamp et al., 2022). This would allow for the construction of a properly weighted selection index to reduce CH_4 without economic losses from reduced performance.

Table 1- Definitions of phenotypic methane traits

Methane Trait	Definition
Methane production rate	CH_4 (g) / d
Methane yield	CH_4 (g) / unit of feed intake
Methane intensity	CH_4 (g) / unit of animal product
Residual methane production	Actual CH_4 (g) – expected CH_4 (g)

Table 2- Heritability estimates of methane production traits in beef and dairy cattle.

Trait	Heritability ± SE	Citation
Methane production (g/d)	0.28 ± 0.06	Hayes et al. 2016[a]
Methane yield (g/kg DMI)	0.20 ± 0.05	Hayes et al. 2016
Residual methane production$_B$[1]	0.19 ± 0.06	Hayes et al. 2016
Residual methane production$_J$[2]	0.19 ± 0.05	Hayes et al. 2016
Residual methane production$_I$[3]	0.19 ± 0.05	Hayes et al. 2016
Residual methane production$_R$[4]	0.19 ± 0.05	Hayes et al. 2016
Methane production (g/d)	0.30 ± 0.06	Manzanilla- Pech et al. 2016[a]
Methane yield (g/kg DMI)	0.20 ± 0.05	Manzanilla- Pech et al. 2016
Methane intensity (g/ kg weight)	0.25 ± 0.06	Manzanilla- Pech et al. 2016
Residual phenotypic methane[5]	0.19 ± 0.05	Manzanilla- Pech et al. 2016
Residual genetic methane[6]	0.15 ± 0.05	Manzanilla- Pech et al. 2016
Methane production (g/d)	0.27 ± 0.07	Donoghue et al. 2016[a]
Methane yield (g/kg DMI)	0.22 ± 0.06	Donoghue et al. 2016
Residual methane production$_B$[1]	0.19 ± 0.06	Donoghue et al. 2016
Residual methane production$_J$[2]	0.19 ± 0.06	Donoghue et al. 2016
Residual methane production$_I$[3]	0.19 ± 0.06	Donoghue et al. 2016
Residual methane production$_R$[4]	0.19 ± 0.05	Donoghue et al. 2016
Methane production (g/d)	0.21 ± 0.06	Lassen & Løvendahl, 2015[b]
Methane intensity (g/ L milk)	0.21 ± 0.06	Lassen & Løvendahl, 2015
CH_4:CO_2	0.16 ± 0.04	Lassen & Løvendahl, 2015
Predicted methane yield (g/kg DMI)[7]	0.12 ± 0.06	van Engelen et al. 2015[b]
Predicted methane yield (g/kg DMI)[8]	0.20 ± 0.07	van Engelen et al. 2015
Predicted methane yield (g/kg DMI)[9]	0.44 ± 0.10	van Engelen et al. 2015
Predicted methane emissions (g/d)[10]	0.13 ± 0.04	Pickering et al. 2015[c]
Predicted methane emissions (g/d)	0.35 ± 0.12	de Haas et al. 2011[b]
Predicted methane emissions (g/d)[11]	0.25 ± 0.01	Kandel et al. 2017[b]

[1]using Blaxter and Clapperton (1965) equations.
[2]using Johnson et al. (1995) equations.
[3]using International Panel on Climate Change (2006) equations.

[4]expected methane production obtained by the regression of methane production rate on DMI.
[5]using Kennedy et al. (1993) equations for the residual phenotypic regressions of a trivariate analysis of MPR, DMI and weight.
[6]using Kennedy et al. (1993) equations for the residual genetic regressions of a trivariate analysis of MPR, DMI and weight.
[7]using Dijkstra et al. (2011) equations.
[8]using Dijkstra et al. (2011) equations excluding fatty acids with a difference >40% between data sets.
[9]using Dijkstra et al. (2011) equations excluding fatty acids with a difference >40% between data sets and with concentrations <1 g/100 g fat.
[10]using de Haas et al. (2011) equations.
[11]using milk mid-infrared spectrometry in first lactation and Vanlierde et al. (2015) equations.
[a]Angus cattle.
[b]Holstein dairy cattle
[c]dairy cows

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