

Review

Relationships between Dietary Chemical Components and Enteric Methane Production and Application to Diet Formulation in Beef Cattle

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Abstract: We used published data consisting of 263 treatment mean observations from beef cattle and dairy steers and heifers, in which CH₄ was measured via chambers or head boxes, to evaluate relationships between enteric CH₄ production and dry matter intake (DMI) and dietary components. Daily DMI was positively related (slope = 15.371, $p < 0.001$) to total daily production (g/d) of CH₄ ($r^2 = 0.821$). Among chemical components, dietary neutral detergent fiber (NDF) concentration was the most highly related ($r^2 = 0.696$; slope = 0.2001; $p < 0.001$) to CH₄ yield (g/kg of DMI), with strong relationships also noted for dietary starch:NDF ratio ($r^2 = 0.662$; slope = -2.4587 ; $p < 0.001$), starch ($r^2 = 0.495$; slope = -0.106 ; $p < 0.001$), and the proportion of metabolizable energy relative to gross energy ($r^2 = 0.561$; slope = -23.663 ; $p < 0.001$). The slope (-0.5871) and intercept (22.2295) for the dietary ether extract vs. CH₄ yield were significant ($p < 0.001$), but the relationship was highly variable ($r^2 = 0.150$). For dietary crude protein concentration, the slope for CH₄ yield was not significant (-0.0344 ; $p < 0.381$) with an r^2 value near zero. Decreasing DMI by programming body weight gain or restricting feed intake could decrease CH₄ production in confined cattle, but these approaches might negatively affect growth performance and product quality, potentially negating positive effects on CH₄ production. Feeding higher-quality forages or using grazing management systems that decrease dietary NDF concentrations or substituting grain (starch) for forage should decrease both CH₄ yield from enteric production and manure CH₄ production via increased digestibility. Effects of feeding management and diet formulation strategies should be additive with other mitigation approaches such as feed additives, allowing the cattle industry to achieve maximal decreases in enteric CH₄ production, while concurrently maintaining optimal beef production.

Keywords: cattle; diet formulation; dietary chemical components; dry matter intake; enteric methane production



Citation: Galyean, M.L.; Hales, K.E. Relationships between Dietary Chemical Components and Enteric Methane Production and Application to Diet Formulation in Beef Cattle. *Methane* **2024**, *3*, 1–11. <https://doi.org/10.3390/methane3010001>

Academic Editor: Secundino López

Received: 5 December 2023

Revised: 28 December 2023

Accepted: 4 January 2024

Published: 9 January 2024



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1. Introduction

Beef cattle production is the single largest agricultural commodity area in the United States, contributing over USD 66 billion in receipts in 2019 [1]. Although cattle can convert low-quality feeds into high-quality protein for human consumption, they are a source of agricultural greenhouse gas emissions to the atmosphere. The agriculture sector in the United States contributes approximately 10% of total greenhouse gas emissions, and livestock contributes 3.8% [2]. Nonetheless, enteric CH₄ emissions are responsible for 30% of the anthropogenic methane budget, highlighting the need for a clear understanding of factors that affect CH₄ production and development of practical mitigation strategies.

Methanogenesis is critical in cattle because it prevents accumulation of metabolic hydrogen in the rumen by serving as a reducing equivalent sink [3]. Alternative hydrogen sinks exist, however, and these alternative sinks are affected by the ingredient and chemical composition of the diet, such that the quantity of CH₄ produced by cattle varies based on

dietary constituents that are fed. Diets that produce acetate liberate hydrogen to be used by methanogenic archaea to produce CH₄. Conversely, propionate serves as a net hydrogen sink, and diets that increase propionate and decrease acetate result in decreased ruminal CH₄ production, reflecting decreased availability of metabolic hydrogen for methanogens to reduce CO₂ to CH₄.

Understanding relationships between various dietary constituents and CH₄ production in cattle will allow for development of strategies to mitigate CH₄ emissions by the cattle industry. Our objective was to evaluate the relationships between enteric CH₄ production and dietary chemical constituents and feed intake using published databases and to relate the findings to diet formulation and management practices that could be used to decrease CH₄ production.

2. Materials and Methods

Mixed model regression methods were used to evaluate the relationship between CH₄ production and DMI and various dietary components using previously published data. The focus of this effort was not to develop prediction equations, but to examine relationships that could then be applied to feeding management strategies and diet formulation practices, thereby providing practical, cost-effective methods for decreasing enteric CH₄ production.

2.1. Description of the Database

The database used to evaluate relationships between enteric CH₄ production and DMI and dietary chemical components was derived from the development and evaluation datasets described by [4,5]. The development dataset consisted of 134 treatment means from 34 respiration calorimetry studies that involved growing and finishing beef cattle and dairy steers and heifers, whereas the evaluation dataset consisted of 129 treatment means from 29 respiration calorimetry studies with beef and dairy steers and heifers. Across the two datasets, measurements of daily CH₄ production were obtained by using chambers (208 studies) or head boxes (55 studies). Dry matter intake and measured CH₄ and energy concentrations (i.e., digestible [DE] and metabolizable [ME] energy) were available for all studies in these two datasets. The average body weight of animals in the combined dataset was 381 kg (range of 134 to 730 kg), with an average DMI of 6.3 kg/d (range of 2.3 to 12.2 kg). Daily CH₄ production averaged 124.7 g/d (range of 25 to 268 g/d), with an average CH₄ yield of 20.1 g/kg of DMI (range of 6.5 to 34.7). The complete development and evaluation datasets are available in spreadsheet format as supplementary material in [4]. As noted previously, the goal of the present analyses was to evaluate relationships, not to produce prediction equations. Thus, to provide the maximum number of observations to achieve this goal, the two datasets were combined to yield 263 observations from 63 studies. Dietary chemical components evaluated (expressed as a percentage of dietary dry matter [DM]) included crude protein (CP), ether extract (EE), neutral detergent fiber (NDF), and starch. Chemical components were calculated from tabular feed composition values for dietary feed ingredients [6] when not reported in the study. For the development dataset, all studies reported CP concentrations, but calculated values for EE, NDF, and starch were used for 46, 7, and 72% of the observations, respectively. For the evaluation dataset, calculated values for CP, EE, NDF, and starch were used for 19, 27, 57, and 64% of the observations, respectively. Because energy concentrations were available for all studies in the database, the relationship between metabolizability (ME concentration divided by gross energy [GE] concentration) and CH₄ production was also evaluated.

2.2. Relationship of Methane Production to Dry Matter Intake and Dietary Components

Because DMI is a major factor affecting enteric CH₄ production [6], initial analyses considered the relationship between DMI (kg/d) and CH₄ production (g/d). Subsequent analyses involving dietary components and metabolizability focused on CH₄ production per unit of DMI (g of CH₄/kg of DMI), often referred to as CH₄ yield. Mixed model methods described by [7] were used to evaluate the relationship between CH₄ production

as the dependent variable and DMI and the selected dietary composition variables. Random intercept and slope effects associated with the 63 studies were included for all models. The covariance structure used for these analyses was unstructured, and the estimation method was restricted maximum likelihood. Study-adjusted data were created for each data point from the linear models as described previously [8]. The coefficient of determination (r^2) and root mean square error (RMSE) were determined for the model using the study-adjusted values and PROC MIXED and PROC REG of SAS (SAS Inst. Inc., Cary, NC, USA, version 9.3).

3. Results and Discussion

3.1. Relationships of Methane Production to Dry Matter Intake and Dietary Chemical Components

Results of the mixed model regression analyses are shown in Table 1, with graphical representations of the relationships shown in Figure 1. As mentioned previously, because of the importance of DMI as a driver of enteric CH_4 production, initial analyses involved regression of daily CH_4 production on DMI. As expected, the relationship between these two variables was strong, with DMI accounting for 82.1% of the variation in daily CH_4 production (Table 1; Figure 1A). Dry matter intake has consistently been identified as a key component of equations to predict CH_4 production in cattle [9–12], with DMI alone often yielding prediction equations that are equivalent in accuracy and precision to more complex equations.

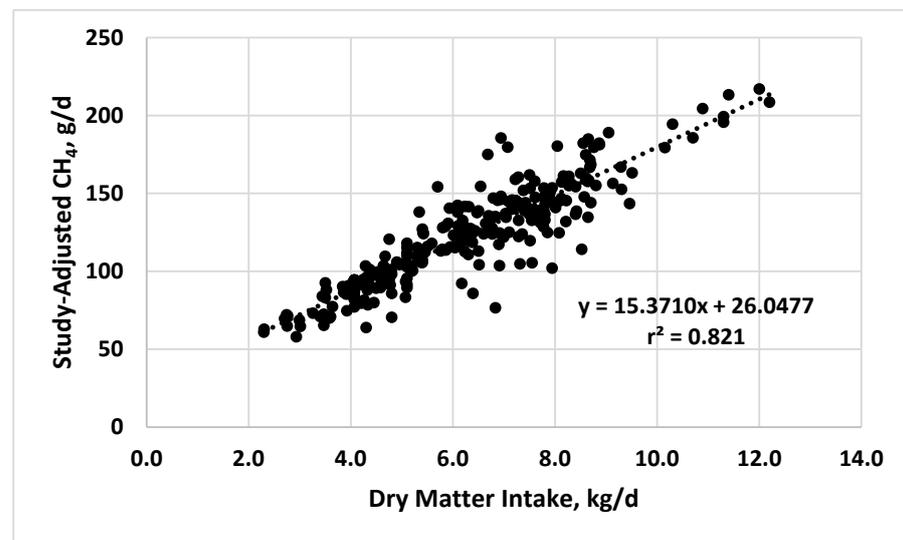
Table 1. Relationships between study-adjusted enteric methane production (g/d) and dry matter intake (DMI) and methane production expressed as g/kg of DMI and various dietary chemical components and diet metabolizability developed from a literature database ¹.

Item ²	Regression Coefficients		Regression Statistics	
	Intercept	Slope	RMSE	r^2
	---- CH_4 , g/d ----			
Dry matter intake, kg/d	26.0477	15.3710	13.96	0.821
<i>p</i> -values ³	<0.001	<0.001	CV = 11.39%	
Lower 95% CI	20.2892	14.4950		
Upper 95% CI	31.8062	16.2470		
	---- CH_4 , g/kg of DMI ----			
Crude protein, %	20.2005	−0.0344	2.53	0.003
<i>p</i> -values ³	<0.001	0.381	CV = 12.82%	
Lower 95% CI	19.0317	−0.1115		
Upper 95% CI	21.3694	0.0428		
Ether extract, %	22.2295	−0.5871	2.31	0.150
<i>p</i> -values ³	<0.001	<0.001	CV = 11.57	
Lower 95% CI	21.5201	−0.7577		
Upper 95% CI	22.9390	−0.4165		
Neutral detergent fiber, %	13.5959	0.2001	2.02	0.696
<i>p</i> -values ³	<0.001	<0.001	CV = 9.65	
Lower 95% CI	12.9563	0.1840		
Upper 95% CI	14.2355	0.2162		
Starch, %	23.4214	−0.1060	2.04	0.495
<i>p</i> -values ³	<0.001	<0.001	CV = 9.89	
Lower 95% CI	22.9950	−0.1191		
Upper 95% CI	23.8478	−0.0929		
Starch:neutral detergent fiber ratio	22.7962	−2.4587	2.18	0.662
<i>p</i> -values ³	<0.001	<0.001	CV = 10.91	
Lower 95% CI	22.4363	−2.6730		
Upper 95% CI	23.1561	−2.2444		

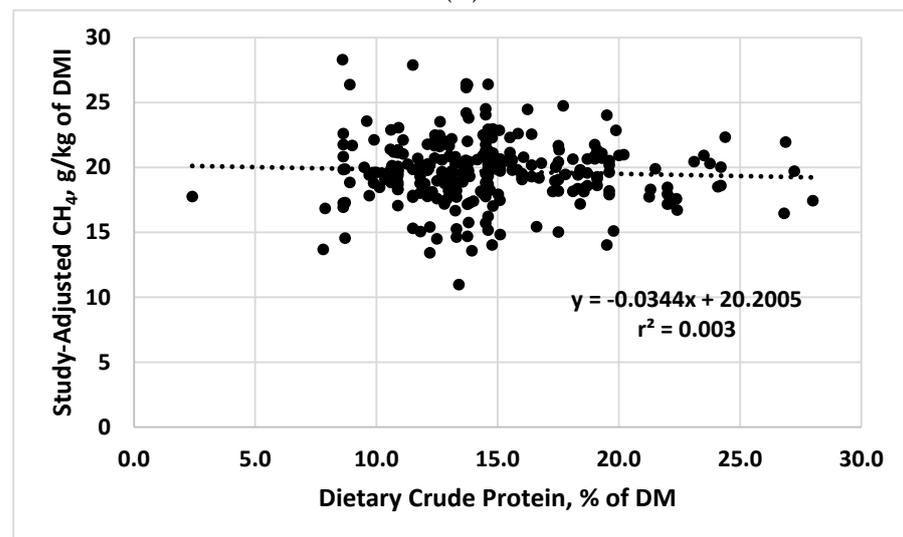
Table 1. Cont.

Item ²	Regression Coefficients		Regression Statistics	
	Intercept	Slope	RMSE	r ²
Metabolizability	34.8909	−23.6630	1.84	0.561
<i>p</i> -values ³	<0.001	<0.001	CV = 8.80	
Lower 95% CI	33.3687	−26.2140		
Upper 95% CI	36.4131	−21.1120		

¹ Data were adjusted for random intercepts and slopes associated with the 63 studies in the database. ² Dietary chemical composition data were expressed on a dry matter basis. Metabolizability = metabolizable energy divided by gross energy. ³ Probability that the intercept and slopes differ from zero; CV = RMSE divided by the overall mean of dry matter intake, dietary chemical components, and metabolizability, expressed as a percent; r² is not adjusted for the number of parameters in the model.

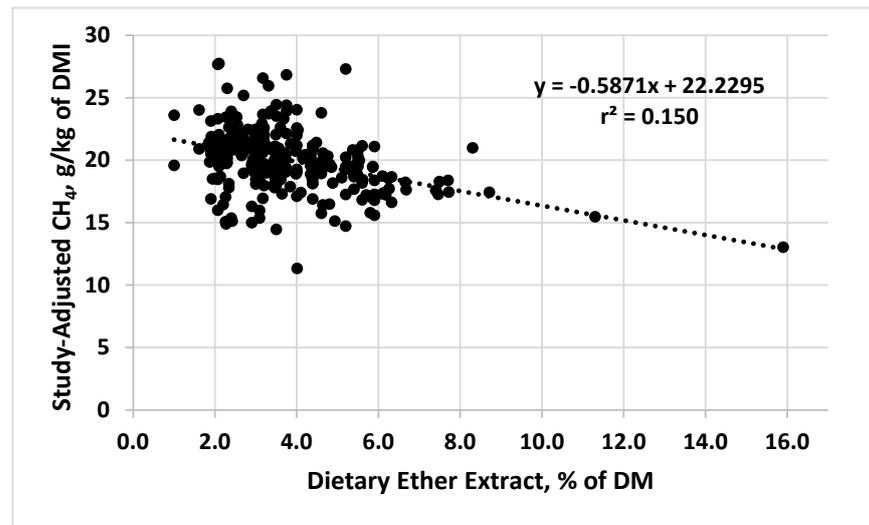


(A)

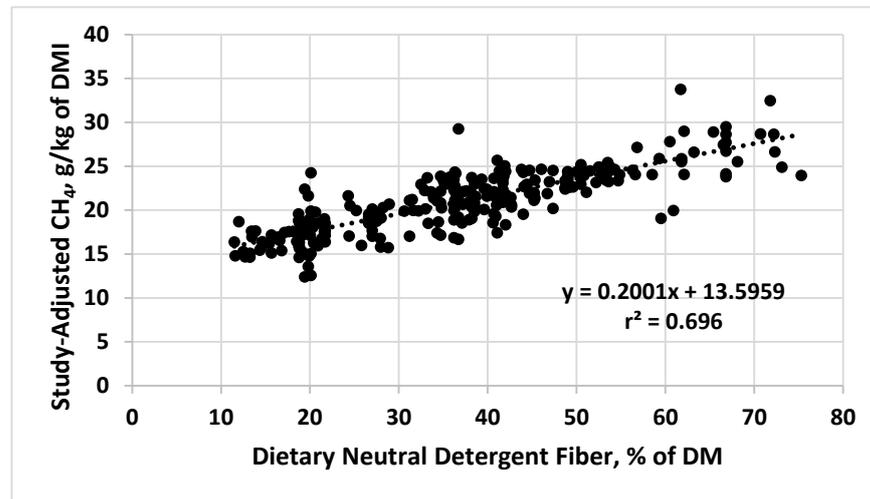


(B)

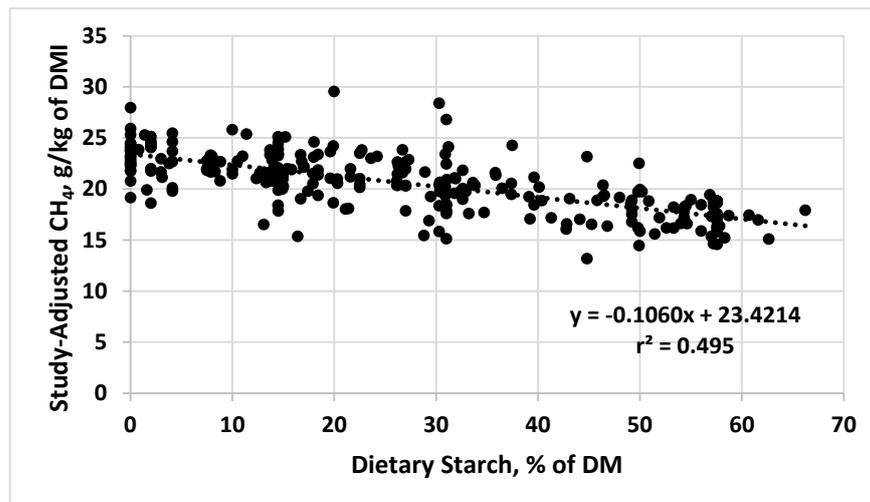
Figure 1. Cont.



(C)



(D)



(E)

Figure 1. Cont.

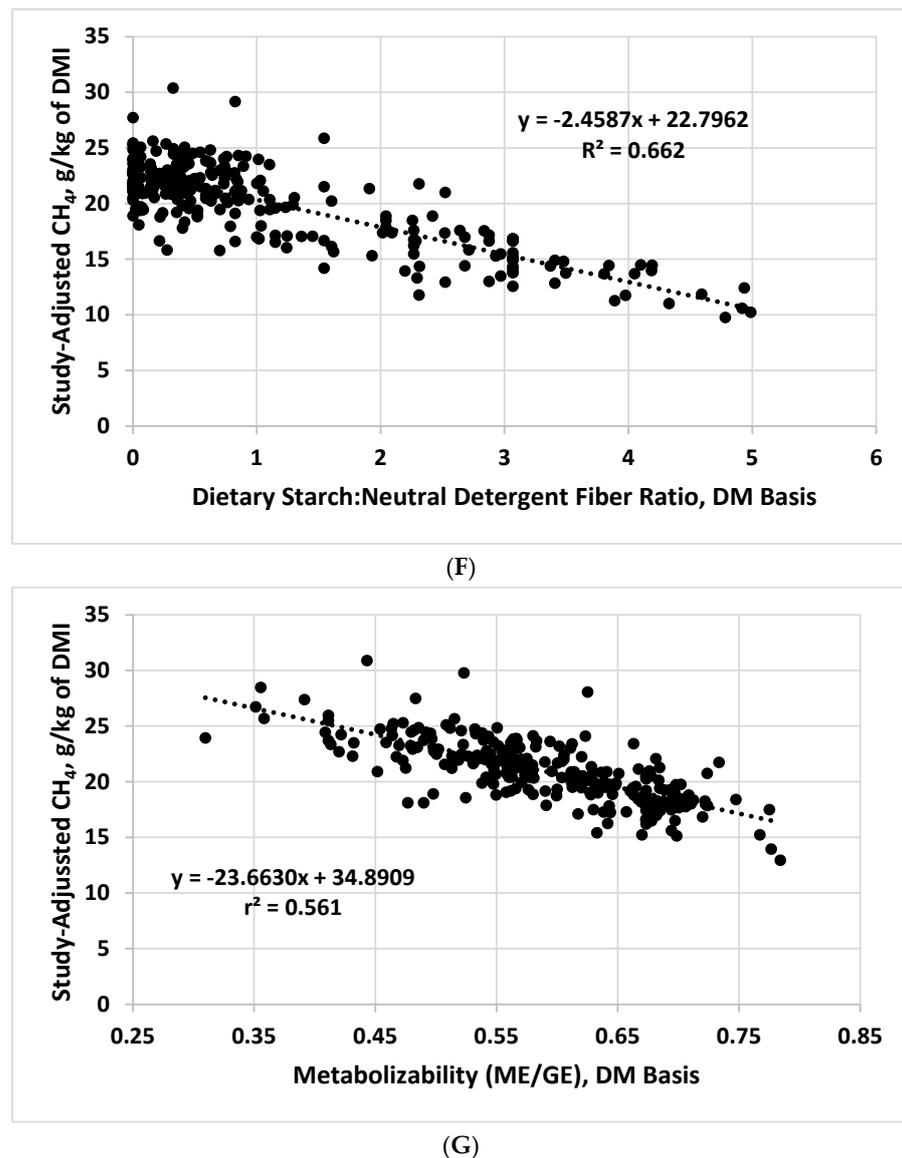


Figure 1. Relationships between study-adjusted enteric methane production (g/d or g/kg of dry matter intake) and dry matter intake DMI; (A), dietary crude protein (B), ether extract (C), neutral detergent fiber (D), starch (E), starch:neutral detergent fiber ratio (F), and diet metabolizability (metabolizable energy/gross energy; (G) developed from a literature database.

Given the importance of DMI as a driver of enteric CH_4 production, analyses of the effects of various dietary components focused on CH_4 production relative to DMI (i.e., CH_4 , g/kg of DMI), which, as noted previously, is typically referred to as CH_4 yield [10]. Across the wide range of dietary CP concentrations in the dataset (average of 14.6% of dietary DM, with a range of 2.4 to 28%), there was essentially no relationship to CH_4 yield, with CP concentration accounting for only 0.3% of the variation in CH_4 yield, with a non-significant ($p = 0.381$) slope of the regression equation (Table 1; Figure 1B). Jennings et al. [13] reported no difference in CH_4 production as a percentage of GE or DE in beef steers fed diets with 13.8 vs. 19.5% CP. Likewise, increasing the level of fishmeal supplementation in dairy heifers fed straw-based diets did not affect CH_4 production [14].

The EE concentration in the combined dataset averaged 3.82% of the dietary DM, with a range of 1 to 15.9%. The slope of the relationship between dietary EE concentration and CH_4 yield was significant ($p < 0.001$), but the r^2 was only 0.15 (Table 1). As is evident from the graphical relationship between CH_4 yield and EE (Figure 1C), the negative slope

associated with EE seemed to be strongly influenced by a small number of datapoints from diets with very high ether extract concentrations, which are known to decrease DMI and NDF digestibility [6]. Nonetheless, removal of the three datapoints from the study associated with these high values did not appreciably change the intercept or slope of the study-adjusted data and only slightly decreased the r^2 (0.105). Thus, within dietary EE concentrations ranging from approximately 2 to 6%, one would expect CH_4 yield to generally decrease with increasing dietary EE concentrations, but responses would likely be highly variable. Using studies conducted with beef and dairy cattle and lambs, Beauchemin et al. [15] reported that each 1% increase in dietary EE decreased CH_4 yield by 5.6%. Based on the observed slope and the overall mean for CH_4 yield in our database, CH_4 yield was decreased by 2.9% for each 1% increase in dietary EE concentration. Using specific fat sources could elicit more consistent responses, as adding 3.4 g of fat/kg of dietary DM from tallow, sunflower oil, and sunflower seeds to high-forage diets decreased CH_4 production at equal DE intake by approximately 15% in beef heifers [16]. Because of the negative effects of added fat on ruminal fiber digestion, the potential to mitigate CH_4 via added fat has limits, with the practical viability of this approach depending on whether the added energy from fat offsets negative effects on fiber digestion [15].

The average dietary NDF concentration in the combined dataset was 36.6%, with a range of 11.5 to 75.3% of the dietary DM. As dietary NDF concentration increased, CH_4 yield increased, with the strongest relationship to CH_4 yield ($r^2 = 0.696$) of any of the dietary composition variables we evaluated (Table 1; Figure 1D). The effect of dietary NDF concentration is related to its negative relationship with dietary concentrate level—as grains replace forages in the diet, NDF decreases and starch increases, with a resulting decrease in CH_4 production [17,18]. Although this relationship is straightforward for grains and traditional forages/coarse roughages, many grain byproducts have a relatively high NDF concentration, which might complicate the relationship between dietary NDF and CH_4 production. Nonetheless, many of the datapoints in our combined database included diets with high levels of grain byproducts, suggesting that these feed sources might respond similarly to traditional roughage sources in terms of the relationship between NDF and CH_4 yield.

Starch concentration in the combined dataset averaged 26.6% of the dietary DM, with a range of 0 to 66.2%. As expected from the inverse association between dietary concentrations of NDF and starch, CH_4 yield decreased as starch concentration increased (Figure 1E). The relationship was not, however, as strong as the relationship between CH_4 yield and dietary NDF concentration ($r^2 = 0.495$ vs. 0.696). Increasing dietary starch is associated with decreased CH_4 because of shifts in volatile fatty acids, particularly propionate, which competes with CH_4 as sink for metabolic hydrogen [19]. In addition, increasing the proportion of grain and thereby starch content in diets increases microbial lipid synthesis by ruminal microbes [20], providing another potential sink for ruminal metabolic hydrogen [21].

Using the development dataset and testing derived prediction equations with the evaluation dataset, Galyean and Hales [5] reported that the starch:NDF ratio was selected in a stepwise regression to predict CH_4 yield over the individual values of starch and NDF. Use of the ratio, with or without dietary EE concentration, resulted in r^2 values when applied to the evaluation dataset that ranged from 0.73 to 0.77. Thus, we expected that when evaluated in the combined dataset, the starch:NDF ratio would be among dietary variables that are the most highly related to CH_4 yield. The average starch:NDF ratio in the combined dataset was 1.14, with a range of 0 to 4.99. Although the relationship was relatively strong (Figure 1F), the r^2 for the regression of CH_4 yield on the starch:NDF ratio was less (0.662) than the r^2 for dietary NDF concentration alone (0.696; Table 1). These results suggest that the dietary starch:NDF ratio might not offer major advantages in predicting CH_4 yield compared with dietary NDF concentration, but current analyses do not consider associations among dietary constituents that might affect their predictive ability.

As noted previously, direct measures of GE and ME were available for all values in the combined dataset. The resulting metabolizability values in the combined dataset averaged 0.59, with a range 0.31 to 0.78. Yan et al. [22] had previously demonstrated a significant relationship between metabolizability and CH₄ yield; thus, we also evaluated this relationship (Table 1; Figure 1G). Indeed, the r^2 value of 0.561 for the regression of CH₄ yield on metabolizability was indicative of a strong relationship, suggesting that it could be a useful component of prediction equations for CH₄ yield. Whether tabular values of metabolizability for feedstuffs would have a similar relationship as the directly measured values in our dataset will need to be evaluated.

3.2. Managing Methane through Feeding Intake Management Strategies

Energy requirements of ruminant livestock are sufficiently well defined to allow “programming” of DMI to meet the needs for a given level of production. Because of the importance of DMI as a driver of enteric CH₄ production, the use of restricted feeding to limit over consumption or programmed feeding to achieve a particular rate of body weight gain for feedlot beef cattle might offer a potential avenue for the feedlot industry to decrease CH₄ production [23]. In addition to decreasing enteric CH₄, feeding management approaches that decrease DMI would be expected to decrease fecal output, thereby also decreasing CH₄ losses via manure [23]. Moreover, effects of decreasing DMI through feeding management should be additive with other CH₄ mitigation approaches such as feed additives that inhibit methanogenesis. Nonetheless, for feedlot cattle, decreasing DMI also carries a risk of extending the days on feed to reach a particular carcass weight and composition endpoint or negatively affecting meat quality indices like marbling. Such increases in the length of the feeding period or decreased product quality could affect the economics of production and potentially negate decreases in enteric and manure CH₄ production associated with management of feed intake, requiring careful evaluation of this approach as a CH₄ mitigation strategy. An alternative to managing DMI as a mitigation strategy would be the selection of more efficient animals (e.g., cattle with low residual feed intake) [24]. Unfortunately, in the commercial feedlot industry the genetic background of growing and finishing cattle is rarely known, and there is no practical tool for quickly determining residual feed intake. Thus, an approach based on genetic selection for greater efficiency to decrease CH₄ will require a long-term commitment by the seedstock industry to include measures such as residual feed intake and CH₄ yield in selection indices.

Opportunities to modify CH₄ through management of DMI in lactating dairy cattle are likely more limited than for feedlot cattle. Feeding higher concentrate diets could decrease CH₄ production in lactating dairy cows, both through altered ruminal fermentation shifting metabolic hydrogen away from CH₄ and through decreased DMI needed to maintain desired production levels. Nonetheless, decreasing the level of NDF from roughage to allow for lower DMI would likely have a negative effect on milk quality, specifically milk fat content and would possibly have negative effects on animal health through an increased risk of acidosis, rumenitis, and systemic inflammation [24–26]. Thus, although management of DMI to lower CH₄ production offers possibilities in lactating dairy cows, it would need to be combined with other dietary formulation and feed additive strategies for successful application in practice.

3.3. Applications to Diet Formulation for Mitigation of Methane Emissions

Based on the results of our regression analyses discussed previously, the key dietary factors to consider in formulation strategies to decrease enteric CH₄ production would be concentrations of NDF, starch, and diet metabolizability, with dietary EE concentration being of lesser importance and dietary CP concentration having virtually no effect. Practically, these key factors are often interrelated in terms of diet formulation. Mixed diets with decreased NDF concentration often have increased starch concentration (i.e., a decreased forage and increased grain), which also results in an increased ME concentration and thereby increased metabolizability. For confined cattle fed mixed diets, changing the

forage:concentrate ratio is widely recognized as a feasible CH₄ mitigation strategy [24]. Nonetheless, changes in these key factors can occur in all types of ruminant diets and production situations and are not always a function of the forage-to-concentrate ratio.

With all-forage diets for example, a variety of factors affect NDF concentration, including forage type and maturity. More digestible forages decreased CH₄ yield in dairy cattle and sheep, but effects were less clear for beef cattle [27]. Nonetheless, increased forage quality generally decreases CH₄ production per unit of animal product because DMI and animal production typically increase as forage quality increases [24]. Increased digestibility of higher-quality forages also would be expected to decrease manure CH₄ losses. Type of forage can be important, as greater CH₄ yield was reported for C4 vs. C3 grasses and warm-season legumes [28]. Accordingly, any approach that increases forage quality, including type of forage, grazing management, harvesting forage at earlier maturities, and forage processing that increases digestibility would be expected to affect CH₄ yield, but more data are needed to accurately predict responses.

As noted previously, feeding diets with a greater concentration of starch is a repeatable approach to decrease CH₄ yield and should also decrease CH₄ associated with manure. Starch generally decreases enteric CH₄ because methanogens are sensitive to low ruminal pH [29] and feeding starch results in a lower ruminal pH than feeding all-forage diets [15]. Even so, Beauchemin et al. [24] observed that the global capacity to increase grain feeding to ruminants is limited, so using increased dietary starch as a mitigation tool is limited to production systems in which grains are normally fed at high levels. Grain type (e.g., horny vs. flourey endosperm) also can affect starch digestion [30], with lesser starch digestion with a greater proportion of horny endosperm, although steam flaking can offset the negative effects of endosperm type [30]. Heat and moisture processing methods like steam flaking increase gelatinization of starch and increase the ruminal proportion of propionate and decrease ruminal pH, thereby decreasing CH₄ yield [30,31].

Although adding dietary fat sources has been extensively studied as a tool for decreasing CH₄ yield [24], and our regression analyses showed a negative relationship between dietary EE concentration and CH₄ yield, the relationship was highly variable and of low predictive value. With potential negative effects of fat on fiber digestion noted previously, as well as relatively high cost of fat sources, careful consideration should be given to the total concentration of fat in the diet, as well as to the sources of fat added to the diet.

It should be noted that for practical implementation of any dietary formulation approach to mitigate CH₄ yield, feed mixing and delivery, as well as potential sorting of feed by animals are issues of concern. If diets are inadequately mixed, thereby resulting in the consumption of feed with variable concentrations of particular nutrients, benefits of dietary mitigation strategies would be decreased. Similarly, diets or feeding practices that promote sorting of feed ingredients by groups of cattle could negate the effects of dietary management strategies. For example, based on our results, cattle that sort out ingredients with a greater NDF concentration would likely have increased CH₄ yield compared with cattle that do not sort ingredients and consume something closer to the formulated diet.

4. Summary and Recommendations for Further Research

Our results support the important role of DMI as a driver of enteric CH₄ production in cattle and other ruminant livestock. Among the dietary components we evaluated, concentrations of NDF and starch, as well as metabolizability of the diet were most strongly related to CH₄ production per unit of DMI. To the extent possible within a particular production system, formulating diets to lower concentrations of NDF and increasing starch and metabolizability of the diet would be expected to decrease CH₄ yield. Careful attention to feed mixing and delivery practices to ensure consumption of diets with uniform nutrient concentrations is necessary for diet formulation strategies to be effective. Managing DMI by programmed feeding to achieve a particular body weight gain or small restrictions in feed intake to prevent over consumption also could offer opportunities to decrease enteric CH₄ production, but care must be taken not to negatively affect animal growth and product

quality. Overall, formulation approaches combined with practices that manage DMI could yield practically relevant decreases in CH₄ production when applied to intensive cattle production systems. Moreover, these practices should be additive to other mitigation strategies such as feed additives that decrease CH₄ production.

Author Contributions: Conceptualization, M.L.G. and K.E.H.; Writing, review, and editing, M.L.G. and K.E.H.; Statistical analyses, M.L.G. All authors have read and agreed to the published version of the manuscript.

Funding: This contribution received no external funding.

Institutional Review Board Statement: Not applicable. The study did not involve the use of live animals.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data used for analyses reported in this article have been previously published online as noted in the text.

Conflicts of Interest: The authors declare no conflicts of interest.

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