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Original Research Article

Dietary fat and carbohydrate-balancing the lactation performance and methane emissions in the dairy cow industry: A meta-analysis

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A B S T R A C T

For the agroecosystems of the dairy cow industry, dietary carbohydrate (starch, neutral detergent fiber [NDF]) and fat could directly affect rumen methane emissions and host energy utilization. However, the relationships among diet, lactation performance, and methane emissions need to be further determined to assist dairy farms to adjust diet formulations and feeding strategies for environmental and production management. A meta-analysis was conducted in the current study to explore quantitative patterns of dietary fat and carbohydrate at different levels in balancing lactation performance and environment sustainability of dairy cows, and to establish a methane emission prediction model using the artificial neural network (ANN) model. The results showed that the regression relationship between dietary fat, carbohydrate and methane emissions could be shown by the following models: methane $= 106.78 + (14.86 \times \text{DMI})$, $R^2 = 0.80$; methane $= 443.17 - (46.41 \times \text{starch/NDF})$, $R^2 = 0.76$; and methane $= 388.91 + (31.40 \times \text{fat}) - (5.42 \times \text{fat}^2)$, $R^2 = 0.80$. The regression relationships between dietary fat, carbohydrate and lactation performance could be shown by the following models: milk fat yield $= 1.08 + (0.43 \times \text{starch/NDF}) - [0.34 \times (\text{starch/NDF})^2]$, $R^2 = 0.79$; milk protein yield $= 0.68 + (0.15 \times \text{fat}) - (0.016 \times \text{fat}^2)$, $R^2 = 0.82$. In the structural equation model, we found that when formulating dietary carbohydrates and fats, it was necessary to balance the relationship between methane emissions and lactation performance. Specifically, dietary starch/NDF was lower than 0.63 (extremum point) and dietary fat was between 2.89% and 4.69% (extremum point), it could ensure that the aim of methane emission reduction (methane emissions decrease with increasing dietary starch/NDF and fat) was achieved without losing lactation performance of dairy cows (lactation performance increase with increasing dietary starch/NDF and fat). Finally, we established the ANN model to predict methane emissions (training set: $R^2 = 0.62$; validation set: $R^2 = 0.61$).

1. Introduction

The global warming potential of methane is 28 times higher than CO_2. Hence it is mentioned in the 'United Nations Framework Convention on Climate Change' that methane is one of the six gases, which should be taken international measures (Maasakkers et al., 2019). Therein, livestock farming contributes markedly to global methane emissions. Global methane emissions from agricultural livestock had a 1.9-fold increase from 1961 to 2017 (Eshel et al., 2014). Moreover, methane emissions also seriously reduce the feed conversion efficiency of dairy cows. It has been found that in comparison to dairy cows with low milk yield, dairy cows with high milk yield exhibit a significant decrease in rumen methanogens (Xue et al., 2020). Therefore, it is necessary to adopt strategies to optimize dietary formula to reduce methane emissions.

Since methane emission of rumen microorganisms needs energy support, optimizing the type and proportion of dietary energy sources is a direct and effective way to alleviate methane

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emissions. The dietary energy supply to dairy cows mainly comes from carbohydrates (starch, neutral detergent fiber [NDF]) and fats (Aschenbach et al., 2010). Meanwhile, methane emission of rumen microbiota mainly follows a hydrogenotrophic methanogenesis pathway (Tapio et al., 2017). Hence, dietary carbohydrates and fats, which are closely related to hydrogen metabolism, are considered as the main factors to affect methane emissions (Hristov et al., 2013). Specifically, starch-rich diets could promote propionate fermentation in the rumen, which can compete with methanogens for hydrogen to inhibit methane emission. By comparison, fiber-rich diets could promote acetate fermentation, which can produce more hydrogen for methanogens to utilize (Li et al., 2018; Moss et al., 2000). However, starch-rich diets could increase feed costs and the risk of rumen acidosis (Benchaar et al., 2001). Dietary fat reduced methane production in the rumen by reducing hydrogen accumulation through fatty acid biohydrogenation, and by inhibiting the activity of ruminal methanogens (Pragna et al., 2018). Meanwhile, some studies attributed the methane emission reduction of dietary fat to reduced dry matter intake (DMI), because, high fat could inhibit DMI, which reduces methane emissions by reducing energy intake. Eugene et al. (2008) reported a 9 percent reduction in methane production in dairy cows due to supplemental fat, but this was accompanied by a 6.4 percent reduction in DMI, which resulted in no difference in methane per unit of DMI (Eugène et al., 2008). Thus, dietary carbohydrate and fat can affect methane emissions by regulating the fermentation mode of rumen microbiota. However, the relationships between dietary carbohydrate, fat and methane emissions are not well established. Similarly, the impact of the dietary carbohydrate and fat on the lactation performance of dairy cows also needs further evaluation.

Compared with qualitative literature reviews, meta-analysis as a quantitative alternative can provide objective evidence to resolve mixed results in research and evaluate the effect of treatments (Viechtbauer, 2010). For dairy cows, the effect of essential oil (Belanche et al., 2020) and lipid supplementation (Eugène, et al., 2008) on methane emissions and lactation performance was studied by meta-analysis. However, few models have integrated multiple variables to hierarchically explain the relationships among dietary nutrients—lactation performance—methane emissions. Here, we used structural equation models (SEM) to explore the role of dietary carbohydrate and fat in balancing lactation performance and methane emission of dairy cows. Moreover, as the integration of the information science and other disciplines in recent years, artificial neural networks (ANN) were drawn into agriculture system, given that its ability to handle complex and flexible nonlinear relationships without prior assumptions (Mendez et al., 2019). Here, we will also further access feasibility of ANN model in methane prediction.

Therefore, the objective of this study was to 1) illustrate the quantitative patterns of methane emissions from dairy cows fed dietary carbohydrate and fat at different levels by mixed model, 2) explain the role of dietary carbohydrate and fat in balancing lactation performance and methane emission of dairy cows by SEM, 3) evaluate the feasibility of ANN model in methane prediction, and 4) systematically summarize the pros and cons of dietary nutrients on balanced production performance and farm environment sustainability in the dairy cow industry. Overall, this manuscript provides a comprehensive insight on how to use dietary nutrients effectively to promote lactation performance and reduce methane emissions from dairy cows. Meanwhile, this manuscript provides basis for dairy farm management to formulate reasonable dietary formula to promote environmental sustainability and improve economic benefits in the dairy cow industry.

2. Materials and methods

2.1. Data preparation

The main research question of the study was how dietary carbohydrate and fat affected lactation performances and methane emissions in dairy cows. The keywords were used for literature research as follows: "methane" and "dairy cows" following the PRISMA statement guidelines (Moher et al., 2009). The studies in the "PubMed", "Web of Science", and "ScienceDirect" online databases were collected from peer-reviewed journal articles published from January 2000 to December 2022. According to this study objective, we set the PICO principle (participant, intervention, comparison, outcome) (Moher et al., 2009). Finally, a total of 75 articles were included in this study (Table S1). The detailed articles retrieval process, please see Fig. 1.

2.2. Information extraction

According to the aim of this study, we included publications (the first author, year of publication, and publishing journal), sample size, method of methane detection (GreenFeed system, chambers, and sulfur hexafluoride (SF_6)), actual measured value of methane (g/d), DMI (kg/d), lactation performance (milk yield [kg/d], milk fat [%], milk protein [%]), dietary fat (% DM), NDF (% DM), and starch (% DM). The descriptive statistics of data are shown in Table S2. We used pooled SD, which was calculated by multiplying the standard error of the mean (S.E.M.) by the square root of the number of trials (Xu et al., 2020), as the within-group SD.

2.3. Data calculation and analysis

2.3.1. Mixed regression model

In order to quantify the relationships between dietary nutrients, lactation performance and methane emissions, the data obtained were subjected to mixed modeling analysis using the lme4 package in R (Version 4.1.2, https://cran.r-project.org/package=lme4) (Bates et al., 2015). Accordingly, different studies were treated as a random effect whereas dietary carbohydrate (starch and NDF) and fat or the ratio of methane emission to DMI (methane/DMI, g/kg) was considered as a fixed effect. The following model was used (St-Pierre, 2001):

$$Y_{ij} = B_0 + B_1X_{ij} + B_2X_{ij}^2 + s_i + b_iX_{ij} + e_{ij},$$

where Y_{ij} = dependent variable of methane emission (g/d) or lactation performance (4% milk fat correction milk [4% FCM, kg/d], the ratio of 4% FCM to DMI [4% FCM/DMI, kg/kg], milk fat proportion [%] and yield [kg/d], protein proportion [%] and yield [kg/d]), B_0 = overall intercept across all studies, B_1 = linear regression coefficient of Y on X (fixed effect), B_2 = quadratic regression coefficient of Y on X (fixed effect), X_{ij} = value of the predictor variable (dietary starch [% DM], NDF [% DM], the ratio of dietary starch to NDF [starch/NDF], fat [% DM]) or methane/DMI (g/kg), s_i = random effect of study i, b_i = random effect of study i on the regression coefficient of Y on X in study i, and e_{ij} = the unexplained residual error. The linear or quadratic model that had lower P-values and higher R^2 was used in the following analysis.

2.3.2. Meta-analysis

For studies of fat supplementation, we performed the meta-analysis of the included data to explore the impact of fat processing methods on methane emissions using the StataSE 14 (Stata Statistical Software: Release 12; StataCorp LLC, College Station, TX,

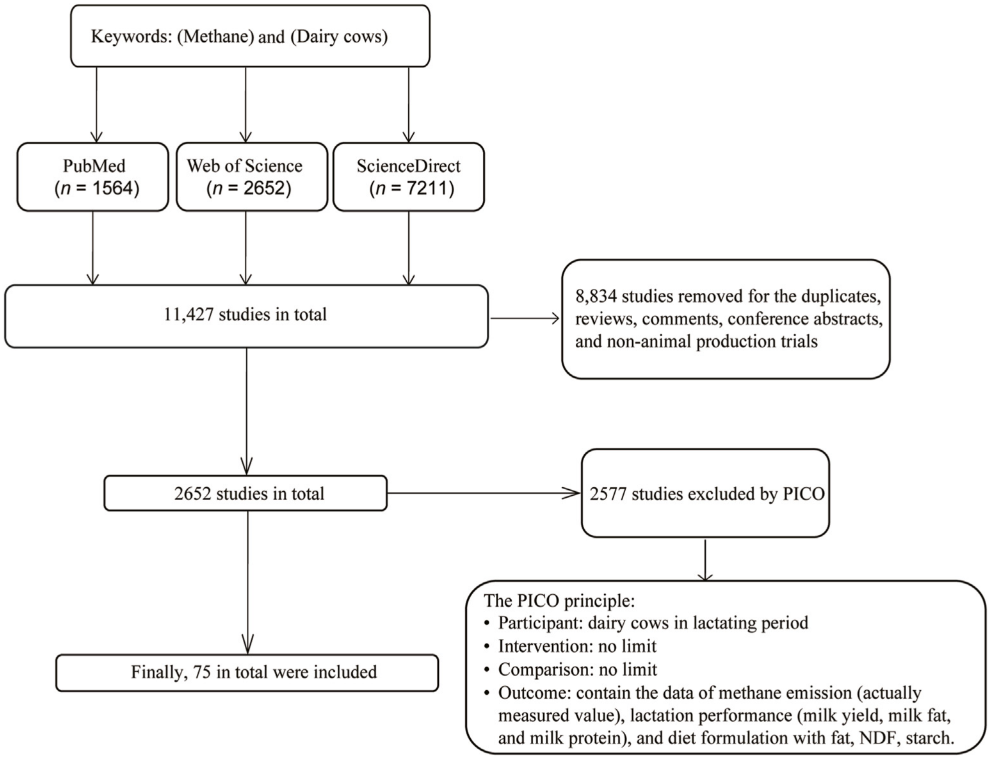

Fig. 1. The flowchart showing the literature retrieval process. The PICO principle included participant, intervention, comparison, and outcome. NDF = neutral detergent fiber.

USA). The Chi-square (χ^2) test and the I^2 statistic were used to measure heterogeneity (Higgins et al., 2002). It was calculated as follows:

$$I^2 = \left[\frac{\chi^2 - (k-1)}{\chi^2}\right] \times 100,$$

where $\chi 2$ is the heterogeneity statistic with Chi-square test and k is the number of studies. And significant heterogeneity was declared at $I^2 > 50\%$ and/or $P_{\text{heterogeneity}} < 0.10$ (Deeks et al., 2019).

The effect sizes included in our study were all continuous variables, hence the standardized mean difference (SMD) was selected as the effect magnitude.

$$\text{SMD} = \frac{\mu_1 - \mu_2}{SP}, \text{SP} = \sqrt{\frac{(n_1-1)SD_1^2 + (n_2-1)SD_2^2}{n_1 + n_2 - 2}},$$

where μ_1 = the mean of fat supplementation group, μ_2 = the mean of control group, SP = combined standard deviation, SD_1 = the standard deviation of fat supplementation group, SD_2 = the standard deviation of control group, n_1 = the sample size of fat supplementation group, n_2 = the sample size of control group (Deeks et al., 2019).

Due to the heterogeneity ($I^2 > 50\%$) for the data about fat supplementation included in our study, the random-effects model was selected as the pooling model. The 95% confidence interval (CI) was calculated and the inverse-variance approach calculates a weighted average as follows:

$$\text{generic inverse} - \text{variance weighted average} = \frac{\sum Y_i\left(1/\text{SE}_i^2\right)}{\sum\left(1/\text{SE}_i^2\right)},$$

where Y_i = the intervention effect estimated in the i study, SE_i = the standard error of that estimate, and the summation is across all studies (Deeks et al., 2019).

2.3.3. Structural equation model

SEM was constructed to evaluate the relationship among dietary nutrients, methane emissions and lactation performance. The goodness-of-fit of the SEM was checked using the χ^2 test, root mean square error (RMSE), and the comparative fit index (CFI). The model had a good fit when the CFI value was close to 1 and the P-values of the statistics were high (traditionally, >0.05) (Schermelleh-Engel et al., 2003). SEM was conducted using the Lavaan package in R (Version 4.1.2, https://cran.r-project.org/package=lavaan) (Cheung, 2015).

2.3.4. Artificial neural network model

ANN consists of three main components: an input layer, a series of hidden layers and an output layer (Li et al., 2019). Therein, the hidden layers are composed by neurons (nodes) (Margenot et al., 2020). The number of hidden layers in ANN is dependent on the complexity of the relationships between inputs and target outputs.

The Neural Network procedure in JMP Pro version 14.0 (SAS Institute Inc., Cary NC, USA) was used to develop a series of ANN models. In the current study, the three-layer ANN, using scaled conjugate gradient algorithm, including one input layer, one hidden layer and one output layer. The training data set was normalized using the min−max approach as follows (Nyachoti et al., 2004):

$$x_i' = \frac{x_i - \min(x)}{max(x) - \min(x)},$$

where x_i was the observed value of the ith input data and x_i' was the ith normalized data.

The output layer was methane emission (g/d). Because the input variables were normalized, the predicted output values were rescaled using the minimal and maximal values of the training data as follows:

$$y_i = y_i^{'} \times (max(y) - \min(y)) + \min(y),$$

where y_i was the predicted value of the ith output and y_i' was the ith normalized output data predicted using the ANN model.

The training conditions including a learning rate of 0.1, training epochs of 1000, and the squared penalty method, were adopted in the current study. To increase the reproducibility of the model, the random seed was set as 500. We used hyperbolic tangent function ($tanh(x) = \frac{e^{2x}-1}{e^{2x}+1}$) and radial basis function neural networks ($RB(x) = e^{-x^2}$) (Karlik et al., 2011; Poggio et al., 2001) as activation functions. Moreover, in order to identify the optimal number of neurons (Liu et al., 1996), we compared 1 to 20 neurons of hidden layer. Models with different nodes and activation functions were selected by the R^2 and RMSE and the model with the maximal R^2 and minimal RMSE was considered as the best-fitted ANN model.

3. Results and discussion

3.1. The relationships between dietary carbohydrate, fat and methane emissions in dairy cows

The effects of DMI, carbohydrate (starch and NDF) and fat contents on methane emissions of dairy cow are shown in Table 1. Animal DMI and methane emissions presented a linear relationship, methane = 106.78 + (14.86 × DMI), (R^2 = 0.80, RMSE = 47.69, Fig. 2A). Some emission reduction strategies, such as fat (Rabiee et al., 2012), nitrate (van Wyngaard et al., 2018) or tannin (Alves et al., 2017) supplementation are partly responsible for the decreased DMI.

The rumen fermentation of dietary carbohydrate, mainly starch and NDF, was the main energy supply mode for dairy cows (Abbas et al., 2020). Therein, fiber could increase the number of fibrolytic bacteria, which resulted in increased NDF utilization and elevated hydrogen level for utilization by methanogens (Abbas, et al., 2020; Flint, 2004). By comparison, starch could increase the population of amylolytic bacteria and lactate utilizers, which compete with methanogens for hydrogen (Mohammed et al., 2010). In the mixed model used in our study, methane emission presented a linear relationship with starch content, methane = 441.80 − (1.32 × starch), (R^2 = 0.76, RMSE = 52.74, Fig. 2B) and with starch/NDF, methane = 443.17 − (46.41 × starch/NDF), (R^2 = 0.76, RMSE = 52.34, Fig. 2C). However, there was no relationship between dietary NDF and methane emissions (P > 0.05) (Table 1), which indicates that there may not be a positive correlation between dietary fiber and methane emissions. Interestingly, in vitro experiment (72 h) using rice straw (fiber) as the sole substrate indicated that inoculation of the microorganisms growing on a fiber-rich feed mixture resulted in lower methane and greater acetate and butyrate production compared with the microorganisms growing on a starch-rich feed mixture (Li et al., 2022). There was a greater community of hydrogenotrophic acetogens in the microorganisms growing on a fiber-rich feed mixture might perhaps compete for H_2 with methanogens. Hence increased dietary NDF did not necessarily mean an increased methane emission; rather it depended on the rumen microbial community. In this study, starch/NDF and methane emissions presented a linear relationship, methane = 443.17 − (46.41 × starch/NDF), (R^2 = 0.76, RMSE = 52.34, Fig. 2C), which suggested that starch/NDF selected for the rumen microbiota determined the rumen fermentation mode and methane emissions. It is noteworthy that starch/NDF was a rough indicator to assess rumen metabolism. We suggested that the further studies use the refined rumen health index (rumen degradable starch [RDS]/physically effective NDF [peNDF]) (Li et al., 2014) to assess rumen methane emissions.

For dietary fat, there was a significant quadratic effect with methane emissions, methane = 388.91 + (31.40 × fat) − (5.42 × fat^2), (R^2 = 0.80, RMSE = 47.58, Fig. 2D). The dietary fat supplementation was considered as a common method of methane emission reduction in the dairy cow industry. On the one hand, dietary fatty acids, in particular medium fatty acids (C12 and C14), have certain toxicity to fiber-degrading microorganisms (such as protozoa), which promote rumen propionate fermentation and inhibit methane emissions (Min et al., 2020). On the other hand, unsaturated fatty acids can compete with methaneogens for hydrogen, thereby inhibiting methane emissions (Min et al., 2020). It could be seen that dietary fat supplementation was an effective emission reduction measure. However, the quadratic curve between dietary fat and methane emissions indicates that the emission reduction effect of fat supplementation may only become obvious when the supplemental fat level exceeds 2.89% (extremum point). Several studies with supplemental level being lower than 2.89% showed that dietary fat supplementation reduced methane emissions per kilogram milk or per kilogram DMI, but had no impact on the methane emissions per day (Aguerre et al., 2011; Benchaar, 2020; Børsting et al., 2020). Moreover, the effect of fat supplementation on emission reduction depended on the dietary fatty acid profile, which was closely related to the processing method of dietary fat (Martin et al., 2008). Hence, a subgroup

Table 1
Best-fit models of methane emissions in response to dietary fat and carbohydrate levels of dairy cows.

Response variable (Y)	Predictor variable (X)	n	Model	Intercept			X			X^2			R^2	RMSE
				Coefficient	S.E.M.	P-value	Coefficient	S.E.M.	P-value	Coefficient	S.E.M.	P-value		
Methane, g/d	DMI, kg/d	292	L	106.78	39.18	<0.001	14.86	1.84	<0.001	–	–	–	0.80	47.69
		292	Q	−298.78	166.12	<0.001	55.34	16.21	<0.001	−0.98	0.39	0.112	0.79	47.96
		292	Q	133.20	240.88	<0.001	32.66	26.83	0.217	−0.93	0.74	0.213	0.65	63.35
	Fat, %	292	L	494.96	15.71	<0.001	−19.91	3.15	<0.001	–	–	–	0.79	49.25
		292	Q	388.91	35.44	<0.001	31.40	15.65	0.046	−5.42	1.61	<0.001	0.80	47.58
	Starch, %	292	L	441.80	16.37	<0.001	−1.32	0.65	0.044	–	–	–	0.76	52.74
		292	Q	447.45	24.87	<0.001	−1.98	2.28	0.393	0.017	0.056	0.756	0.76	52.83
	NDF, %	292	L	355.26	38.57	<0.001	1.71	1.07	0.107	–	–	–	0.66	62.36
		292	Q	49.78	170.74	<0.001	18.07	9.00	0.046	−0.21	0.12	0.069	0.67	61.94
	Starch/NDF	292	L	443.17	15.18	<0.001	−46.41	19.27	0.017	–	–	–	0.76	52.34
		292	Q	437.52	21.30	<0.001	−24.27	61.71	0.685	−18.24	48.39	0.714	0.76	52.43

RMSE = root mean square error; S.E.M. = standard error of the mean; DMI = dry matter intake; L = linear model; Q = quadratic model; NDF = neutral detergent fiber; Starch/NDF = the ratio of dietary starch to NDF.

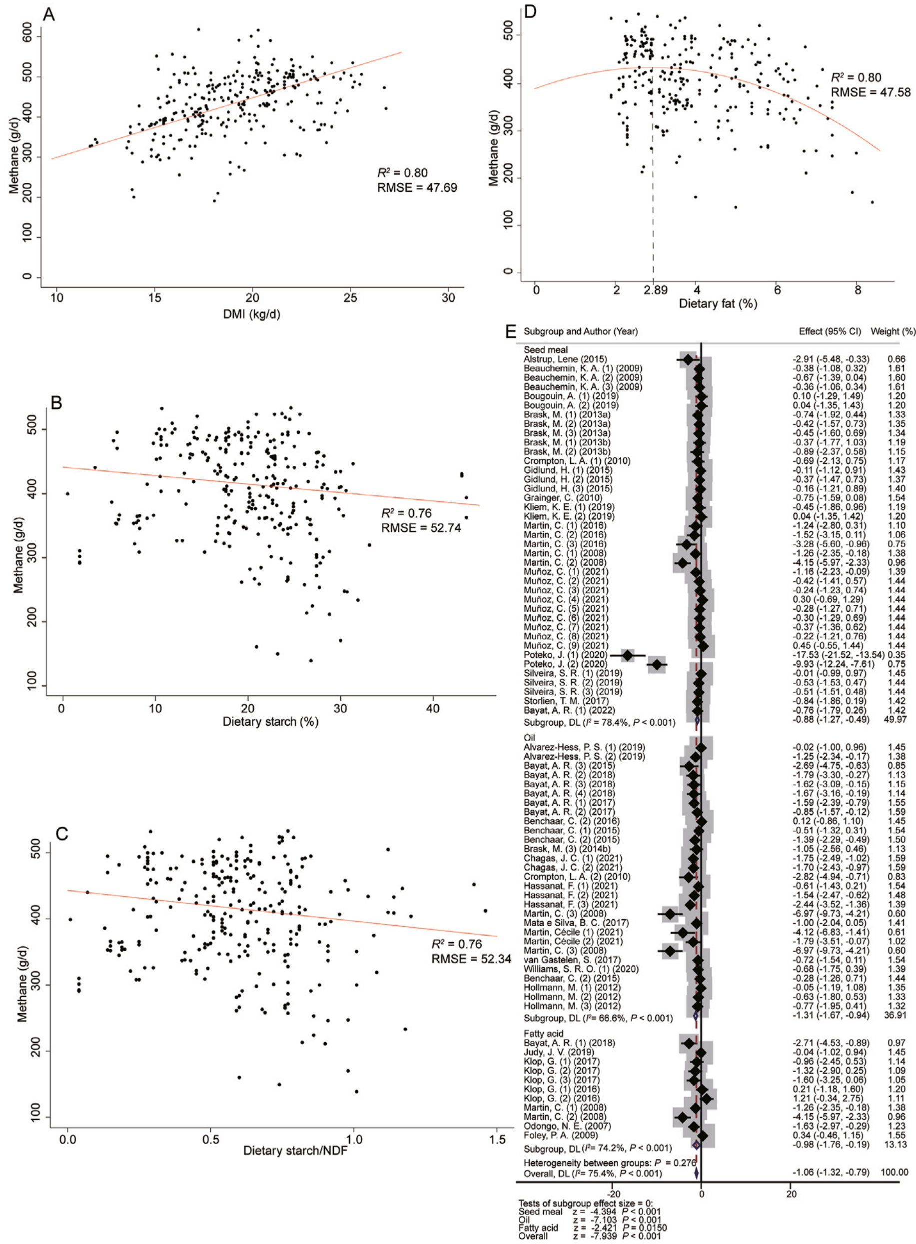

Fig. 2. The relationships between dietary carbohydrate, fat and methane emissions in dairy cows. (A) The regression curve between DMI and methane emissions. (B) The regression curve between dietary starch and methane emissions. (C) The regression curve between dietary starch/NDF and methane emissions. (D) The regression curve between dietary fat and methane emissions. (E) The forest plot of the effects of dietary fat processing methods on methane emissions. RMSE = root mean square error; DMI = dry matter intake; starch/NDF = the ratio of dietary starch to neutral detergent fiber; CI = confidence interval.

analysis is often carried to demonstrate this. For instance, oilseed meal, oil, and fatty acids all had mitigation effects on methane emissions (oilseed meal: $P < 0.001$; oil: $P < 0.001$; fatty acids: $P = 0.015$; Overall: $P < 0.001$), which was consistent with the findings of Martin et al. (2008). However, processing method was not the heterogeneous source of fat supplementation (seed meal: $I^2 = 78.4\%$, $P < 0.001$; oil: $I^2 = 66.6\%$, $P < 0.001$; fatty acids: $I^2 = 74.2\%$, $P < 0.001$; Overall: $I^2 = 75.4\%$, $P < 0.001$) (Fig. 2E).

3.2. The relationships between dietary carbohydrate, fat and lactation performances in dairy cows

It could be seen that the methane emission reduction effects of starch/NDF and fat were significant. Hence, we used dietary starch/NDF and fat contents as predictive factors to evaluate the relationships between dietary nutrients and lactation performance (Table 2). For dietary starch/NDF, there was a quadratic relationship between starch/NDF and 4% FCM, 4% FCM = 28.19 + (6.92 × starch/NDF) − [4.81 × (starch/NDF)^2], ($R^2 = 0.90$, RMSE = 2.27, Fig. 3A). As starch/NDF increased, so was the energy supply used for lactation of dairy cows, leading to an increase in 4% FCM. But when starch/NDF was greater than 0.72 (the extremum point), 4% FCM was decreased, likely because excessive lactic acid cannot be absorbed by the rumen epithelium, causing the decrease of rumen pH and diminishing the number of fiber-degrading bacteria (Shen et al., 2020). Moreover, there was a quadratic relationship between starch/NDF and milk fat yield, milk fat yield = 1.08 + (0.43 × starch/NDF) − [0.34 × (starch/NDF)^2], ($R^2 = 0.79$, RMSE = 51.22, Fig. 3B).

Table 2
Best-fit models of milk performance in response to dietary fat and carbohydrate levels of dairy cows.

Response variable (Y)	Predictor variable (X)	n	Model	Intercept			X			X^2			R^2	RMSE
				Coefficient	S.E.M.	P-value	Coefficient	S.E.M.	P-value	Coefficient	S.E.M.	P-value		
4% FCM, kg/d	Starch/NDF	292	L	29.66	0.92	<0.001	1.12	0.89	0.211	–	–	–	0.90	2.29
		292	Q	28.19	1.13	<0.001	6.92	2.77	0.013	−4.81	2.18	0.028	0.90	2.27
MPY, kg/d		292	L	0.96	0.035	<0.001	0.042	0.049	0.388	–	–	–	0.57	73.15
		292	Q	0.97	0.052	<0.001	0.0092	0.16	0.949	0.027	0.13	0.831	0.57	73.15
MFY, kg/d		292	L	1.19	0.041	<0.001	0.0071	0.062	0.912	–	–	–	0.78	54.68
		292	Q	1.08	0.067	<0.001	0.43	0.21	0.046	−0.34	0.16	0.040	0.79	51.22
MY, kg/d	Fat, %	292	L	30.48	1.02	<0.001	−0.00089	0.15	0.993	–	–	–	0.31	102.31
		292	Q	24.10	1.80	<0.001	3.06	0.73	<0.001	−0.32	0.075	<0.001	0.94	2.09
MPY, kg/d		292	L	0.99	0.038	<0.001	−0.0012	0.0083	0.881	–	–	–	0.58	72.14
		292	Q	0.68	0.091	<0.001	0.15	0.041	0.004	−0.016	0.0043	0.003	0.82	45.14
MFY, kg/d		292	L	1.25	0.052	<0.001	−0.012	0.011	0.297	–	–	–	0.58	76.45
		292	Q	0.76	0.12	<0.001	0.23	0.055	<0.001	−0.026	0.0058	<0.001	0.77	49.88

RMSE = root mean square error; S.E.M. = standard error of the mean; 4% FCM = 4% milk fat correction milk; Starch/NDF = the ratio of dietary starch to neutral detergent fiber; L = linear model, Q = quadratic model; MPY = milk protein yield; MFY = milk fat yield; MY = milk yield.

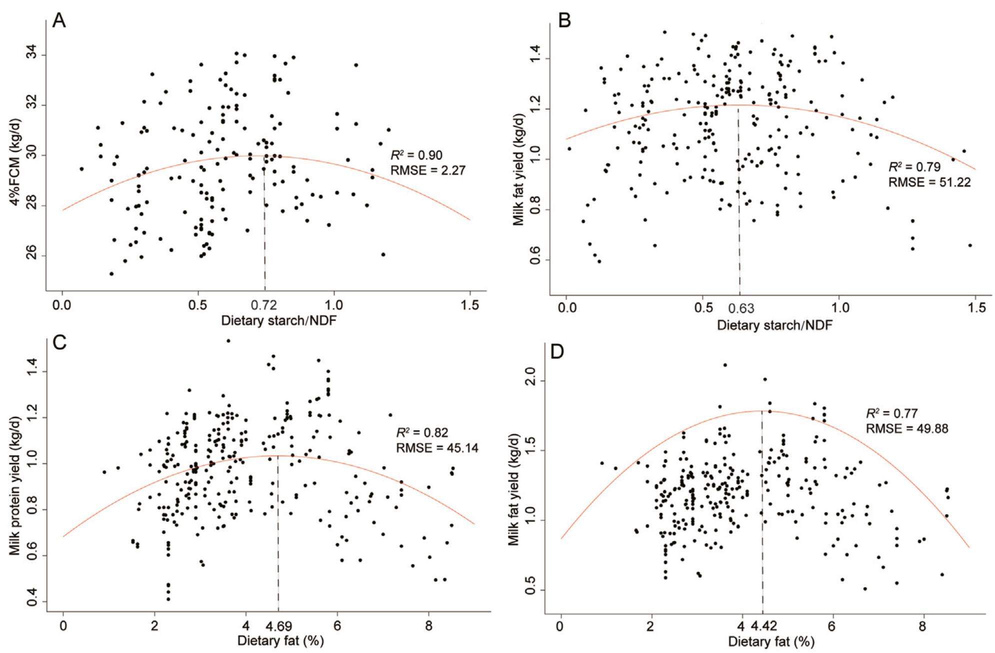

Fig. 3. The relationships between dietary carbohydrate, fat and lactation performances in dairy cows. (A) The regression curve between dietary starch/NDF and 4% FCM. (B) The regression curve between dietary starch/NDF and milk fat yield. (C) The regression curve between dietary fat and milk protein yield. (D) The regression curve between dietary fat and milk fat yield. 4% FCM = 4% milk fat correction milk; starch/NDF = the ratio of dietary starch to neutral detergent fiber; RMSE = root mean square error.

When starch/NDF was greater than 0.63 (extreme point), milk fat yield decreased with increasing starch/NDF levels. High starch/NDF levels would inhibit rumen bacterial growth (*Butyrivibrio fibrisolvens* and *Pseudobutyrvibrio*), which changed the hydrogenation pathway of rumen fatty acids and produced an inhibitory effect on milk fat synthesis trans-10, cis-12 conjugated linoleic acid (CLA), thereby reducing milk fat yield (Zheng et al., 2020).

There was a quadratic relationship between dietary fat and milk protein yield, milk protein yield = 0.68 + (0.15 × fat) − (0.016 × fat^2), (R^2 = 0.82, RMSE = 45.14, Fig. 3C). When dietary fat level was greater than 4.69% (extremum point), milk protein yield decreased with increasing dietary fat level. Although dietary fat has a high energy concentration, high concentrations of polyunsaturated fatty acids can reduce DMI, fiber digestibility, and inhibit rumen fermentation, which may lead to reduced synthesis of microbial proteins and result in reduced milk protein yield (Patra, 2013). There was a quadratic relationship between dietary fat and milk fat yield, milk fat yield = 0.76 + (0.23 × fat) − (0.026 × fat^2), (R^2 = 0.77, RMSE = 49.88, Fig. 3D). When dietary fat was greater than 4.42% (extremum point), milk fat yield decreased with increasing levels of dietary fat. The combination of unsaturated fat acid with hydrogen in the rumen will promote propionate type fermentation, thus inhibiting the production of acetate, which was the precursor of de novo synthesis of fatty acid in the mammary gland (Palmquist et al., 2017).

3.3. The relationship between methane emissions and lactation performances in dairy cows

We used methane/DMI as a predictive factor to explore the relationship between methane emissions and lactation performance (Table 3). There was a linear relationship between methane/DMI and 4% FCM or 4% FCM/DMI, 4% FCM = 40.82 − (0.53 × methane/DMI), (R^2 = 0.90, RMSE = 2.29, Fig. 4A); 4% FCM/DMI = 1.64 − (0.010 × methane/DMI), (R^2 = 0.90, RMSE = 2.79, Fig. 4B). Dairy cow lactation is a process that requires a large

Table 3
Best-fit models of lactation performance in response to methane emissions of dairy cows.

Response variable (*Y*)	Predictor variable (*X*)	*n*	Model	Intercept			*X*			R^2	RMSE
				Coefficient	S.E.M.	*P*-value	Coefficient	S.E.M.	*P*-value		
4% FCM, kg/d	Methane/DMI, g/kg	292	L	40.82	1.72	<0.001	−0.53	0.082	<0.001	0.90	2.29
4% FCM/DMI, kg/kg		292	L	1.64	0.06	<0.001	−0.010	0.0030	<0.001	0.90	2.79
MF, %		292	L	2.86	0.71	<0.001	0.058	0.0080	<0.001	0.78	52.33
MFY, kg/d		292	L	1.31	0.088	<0.001	−0.0050	0.0042	0.238	0.57	70.20
MP, %		292	L	3.23	0.077	<0.001	0.0030	0.0030	0.416	0.55	71.13
MPY, kg/d		292	L	1.21	0.063	<0.001	−0.011	0.0030	<0.001	0.87	41.43

RMSE = root mean square error; S.E.M. = standard error of the mean; 4% FCM = 4% milk fat correction milk; L = linear model; 4% FCM/DMI = the ratio of 4% FCM to dry matter intake; MF = milk fat proportion; MFY = milk fat yield; MP = milk protein proportion; MPY = milk protein yield; Methane/DMI = the ratio of methane emission to dry matter intake.

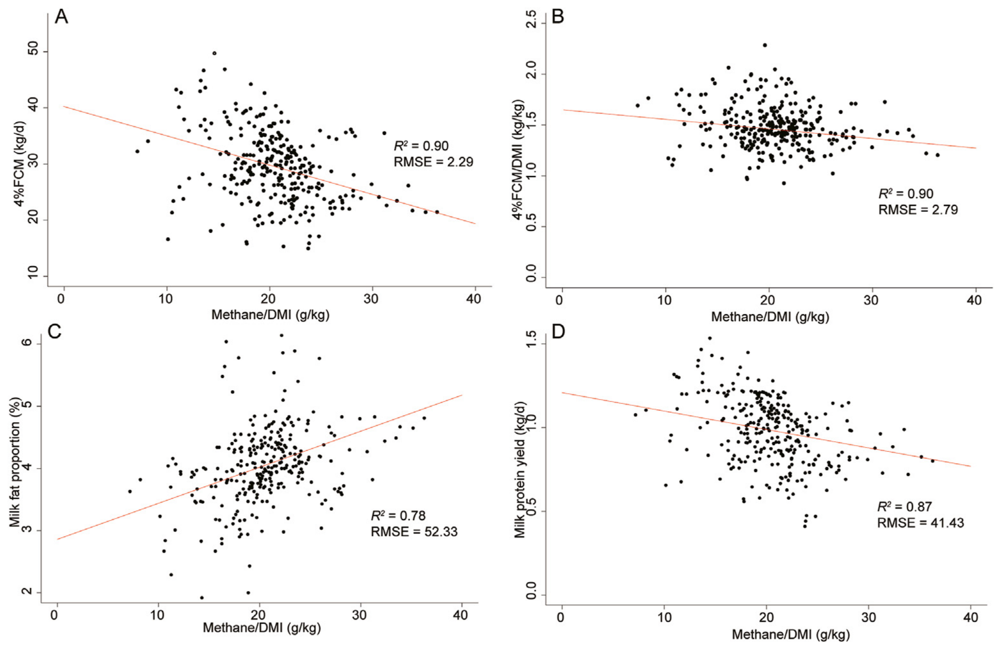

Fig. 4. The relationships between methane emissions and lactation performances in dairy cows. (A) The regression curve between dietary methane/DMI and 4% FCM. (B) The regression curve between dietary methane/DMI and 4% FCM/DMI. (C) The regression curve between methane/DMI and milk fat proportion. (D) The regression curve between methane/DMI and milk protein yield. 4% FCM = 4% milk fat correction milk; Methane/DMI = the ratio of methane emission to dry matter intake; 4% FCM/DMI = the ratio of 4% FCM to dry matter intake; RMSE = root mean square error.

amount of energy supply, and methane emissions inhibits the energy supply to lactation. Energy loss of methane emissions accounts for 2% to 12% of dietary digestible energy (Johnson et al., 1995) and 6.5% to 18.7% of dietary metabolic energy (Appuhamy et al., 2016). If methane emissions per kilogram of standard milk is reduced by 2.5 g, an additional 300 mL of standard milk can be produced per kilogram of DMI (Knapp et al., 2014).

The methane/DMI and milk fat proportion represented a linear relationship, milk fat proportion = 2.86 + (0.058 × methane/DMI), (R^2 = 0.78, RMSE = 52.33, Fig. 4C), which may be attributed to the negative correlation between milk yield and methane emissions. Hence, we further observed the relationship between methane/DMI and milk fat yield. The mixed model showed no relationship between methane/DMI and milk fat yield ($P > 0.05$) (Table 3). For milk protein, there was no relationship between milk protein proportion with methane/DMI ($P > 0.05$) (Table 3) and a linear relationship between methane/DMI and milk protein yield, milk protein yield = 1.21 − (0.011 × methane/DMI), (R^2 = 0.87, RMSE = 41.43, Fig. 4D). Milk protein synthesis is closely related to the rumen energy-nitrogen balance principle (Hall et al., 2008). When energy is wasted in the form of methane, rumen microbial protein synthesis decreases, thereby reducing the substrate for milk protein synthesis.

3.4. The role of dietary carbohydrate and fat in balancing methane emissions and lactation performance in the SEM

We established the SEM based on the dietary elements (fat, starch/NDF), methane emission elements (methane/DMI), and lactation elements (milk yield, milk protein yield, milk fat yield) (Fig. 5A). The elements included in the SEM were all filtered through the mixed model.

In the SEM (Fig. 5A), we found that dietary fat and carbohydrate could positively impact the lactation performance of dairy cows through impacting methane emissions (CFI = 0.100, RMSE = 0.000). Meanwhile, dietary starch/NDF affects both milk fat yield and methane emissions in the SEM. According to the mixed model, when dietary starch/NDF was lower than 0.63 (extremum point), methane emissions decreased while milk fat yield increased (Fig. 5B). Similarly, dietary fat affects both milk protein yield and methane emissions in the SEM. According to the mixed model, when dietary fat was between 2.89% and 4.69% (extremum point), methane emissions decreased while milk protein yield increased (Fig. 5C). Overall, according to SEM, we suggest that when formulating dietary formulas, it is necessary to maximize the effect of methane emission reduction while ensuring that lactation performance of cows is not lost. Meanwhile, we also outline the range of

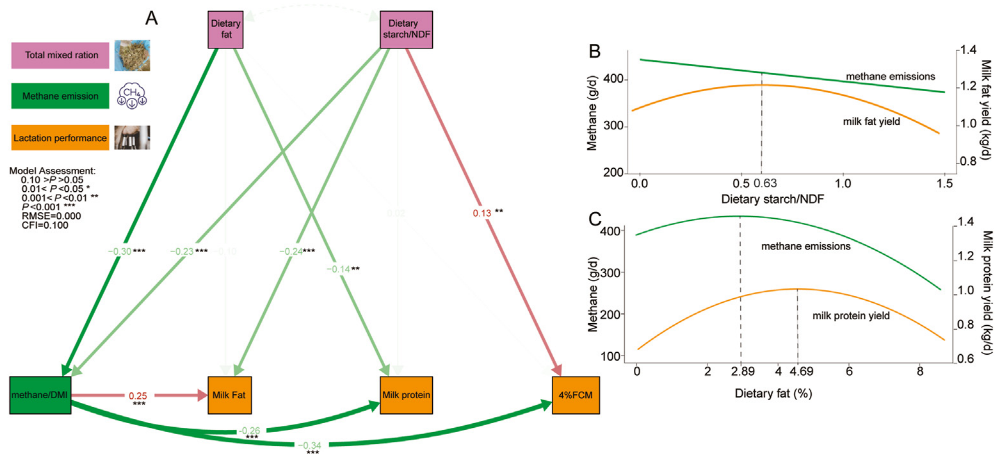

Fig. 5. Balancing dietary carbohydrate, fat between methane emissions and lactation performances in the structural equation models (SEM). (A) The elements included dietary fat, dietary starch/NDF, methane/DMI, milk fat, milk protein, and 4% FCM in SEM. Numbers adjacent to arrows are indicative of the effect size of the relationship. Green arrows represent positive paths and red arrows represent negative paths. Significance levels are as follows: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. (B) The regression curves between dietary starch/NDF and methane emissions (green), and between dietary starch/NDF and milk fat yield (orange). (C) The regression curves between dietary fat and methane emissions (green), and between dietary fat and milk protein yield (orange). RMSE = root mean square error; CFI = comparative fit index; starch/NDF = the ratio of dietary starch to neutral detergent fiber; methane/DMI = the ratio of methane emission to dry matter intake; 4% FCM = 4% milk fat correction milk.

dietary fat and starch/NDF as an approximate guideline. As we used the dietary starch and NDF to establish the model (Fig. S1), only starch/NDF had a significant impact on methane emissions, not starch or NDF alone.

3.5. Establishment of methane emission ANN prediction model

We established a methane emission ANN prediction model using the filtered indicators (dietary fat, starch/NDF, DMI, milk fat proportion, milk protein yield, milk yield and their square) from the mixed models and SEM as mentioned earlier. We used the single hidden layer to establish the ANN model and selected the best model based on R^2 and RMSE (Table 4). The methane emission ANN prediction model contains 12 prediction factors with a hidden layer of 12 nodes (training set: $R^2 = 0.62$, RMSE = 60.01; validation set: $R^2 = 0.61$, RMSE = 54.52; Fig. 6).

With the emphasis on environmental sustainability, carbon taxes and subsidies have gradually become an internationally recognized and typical methane emission reduction constraint and incentive mechanism (Fan et al., 2018). Hence, in order to maximize profit while running a sustainable dairy cow operation, the farmer needs to adjust diet formulation, feeding strategies, and even breeding program based on their understanding of the relationship between methane emissions and lactation performance. However, the measurement of methane emissions requires elaborate instruments (respiration chambers, SF_6 technique, Greenfeed) and a high level of expertise, which is not feasible for large farms (Hristov et al., 2013). Therefore, it is urgent to predict methane emissions based on available indicators. As a supervised learning process, ANN models usually have stronger ability to fit complex nonlinear relationships and higher fault tolerance than linear regression models (Jain et al., 1996). Although the optimal model uses a single hidden layer and a large number of nodes, there is no "over-fitting" according to the difference value of R^2 and RMSE between Training set and Validation set. We believe the ANN model we have established will work in practice. It is worth noting that the construction of the ANN model requires a large sample size. Other researchers (Wang et al., 2022) set up an ANN model using 287 samples to predict daily weight gain and feed conversion ratios. We used 292 samples in our model to predict methane emissions of dairy cows. However, the data in the current study were from previous studies. Unlike the mixed model (the study as random effect), ANN models are unable exclude inter-study influences. But our ANN model used data obtained from farms that had the same methane detection method for animals grazed on a single pasture type to predict methane emissions. Thus, we believe our ANN model will offer a better and more accurate prediction for methane emissions in dairy cows.

Table 4
The performance of artificial neural network (ANN) models with different numbers of nodes and activation functions to predict the methane emissions of dairy cows.[1]

Number of nodes	Hyperbolic tangent function				Radial basis function			
	Training data set		Validation data set		Training data set		Validation data set	
	R^2	RMSE	R^2	RMSE	R^2	RMSE	R^2	RMSE
1	0.33	78.81	0.56	57.82	0.32	79.37	0.58	57.02
2	0.39	75.50	0.57	57.40	0.38	76.10	0.57	57.75
3	0.41	74.05	0.59	55.98	0.42	73.20	0.57	57.40
4	0.51	67.53	0.59	56.41	0.42	73.56	0.56	58.06
5	0.46	70.96	0.62	54.26	0.61	60.68	0.57	57.04
6	0.40	75.03	0.61	54.93	0.49	68.80	0.56	58.29
7	0.54	65.36	0.61	54.88	0.52	67.15	0.58	56.48
8	0.44	72.69	0.63	53.35	0.54	65.54	0.56	57.98
9	0.46	70.94	0.60	55.53	0.63	59.17	0.58	56.57
10	0.47	70.41	0.61	54.42	0.53	66.39	0.61	54.47
11	0.48	69.73	0.61	54.98	0.60	60.89	0.56	58.02
12	0.62[2]	60.01[2]	0.61[2]	54.52[2]	0.53	65.73	0.56	58.20
13	0.57	63.58	0.61	54.98	0.59	61.71	0.57	57.74
14	0.51	67.40	0.62	53.90	0.62	59.51	0.57	57.27
15	0.41	74.44	0.61	54.51	0.35	77.74	0.55	58.76
16	0.60	60.96	0.62	53.66	0.35	77.96	0.57	58.35
17	0.60	61.40	0.62	53.91	0.56	64.48	0.56	58.20
18	0.45	71.58	0.60	55.45	0.63	58.15	0.57	57.68
19	0.42	73.85	0.61	54.50	0.72	51.14	0.56	58.18
20	0.59	61.87	0.61	54.62	0.65	56.76	0.58	56.82

RMSE = root mean square error.
[1] All the ANN models were generated using the data set ($n = 292$).
[2] Means the best performance of ANN models with different numbers of nodes and activation functions to predict methane emissions.

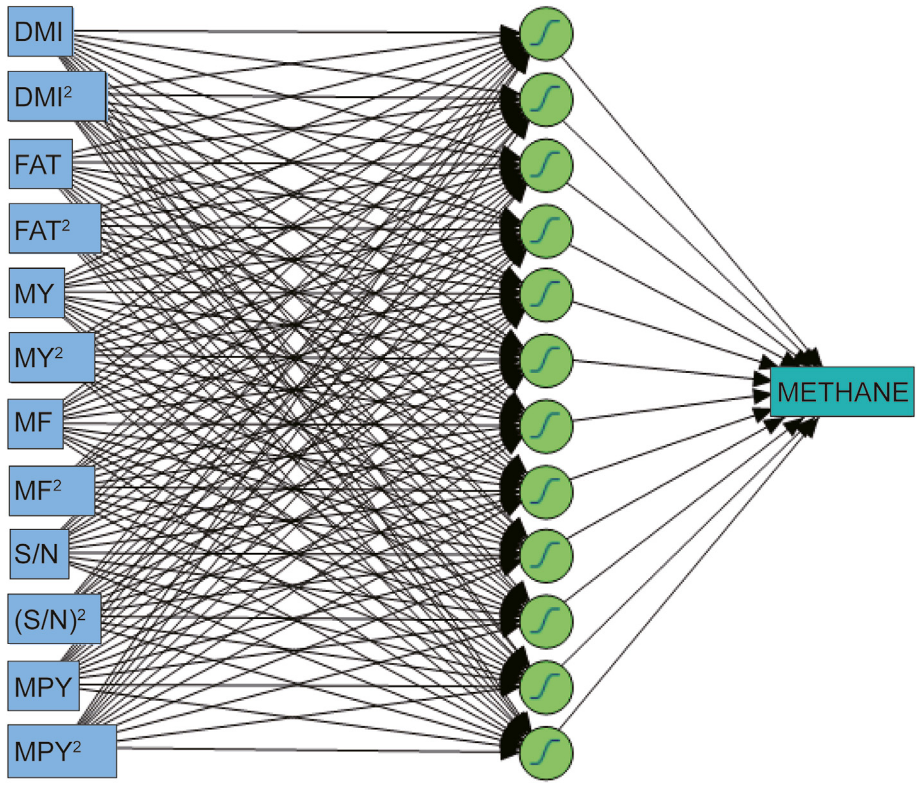

Fig. 6. The best performance of artificial neural network (ANN) models to predict methane emissions. The best ANN model was formed by input layer, hidden layer, and output layer. Input layer included DMI, FAT, MY, MF, S/N, MPY and their square. The hidden layer included 12 nodes and hyperbolic tangent function. Output layer was the methane emissions. DMI = dry matter intake; FAT = dietary fat; S/N = the ratio of dietary starch to neutral detergent fiber; MY = milk yield; MF = milk fat proportion; MPY = milk protein yield.

4. Conclusions

We used a relatively large sample size (n = 292) from 75 articles to explore the effect of dietary carbohydrate and fat on balancing the methane emissions and lactation performance. In the mixed model, DMI, starch and starch/NDF have a linear relationship with methane emissions, with methane = 106.78 + (14.86 × DMI), methane = 441.80 − (1.32 × starch), and methane = 443.17 − (46.41 × starch/NDF), respectively. Moreover, we found that only starch/NDF had a significant impact on methane emissions, not starch or NDF in the SEM. Dietary fat and methane emissions presented a quadratic relationship, methane = 388.91 + (31.40 × fat) − (5.42 × fat^2). When daily dietary fat level was greater than 2.89% (extremum point), there was an obvious reduction of methane emissions. In addition, different processing methods for dietary fat had marked effects on methane emission reduction in the subgroup meta-analysis. Meanwhile, Dietary starch/NDF and milk fat yield presented a quadratic relationship, milk fat yield = 1.08 + (0.43 × starch/NDF) − [0.34 × (starch/NDF)^2], when starch/NDF was greater than 0.63 (extremum point), it would have an adverse impact on milk fat. Dietary fat and milk protein yield represented quadratic relationship, milk protein yield = 0.68 + (0.15 × fat) − (0.016 × fat^2). When dietary fat was greater than 4.69% (extremum point), it would have an adverse impact on milk protein. Methane emissions had a negative relationship with lactation performance, i.e., 4% FCM/DMI (kg/kg) = 1.64 − (0.010 × methane/DMI), milk fat proportion = 2.86 + (0.058 × methane/DMI), and milk protein yield = 1.21 − (0.011 × methane/DMI). The SEM suggested that when formulating dairy cow rations, it is necessary to consider the role of dietary energy sources in the balance between methane emissions and lactation performance. We suggest that when dietary starch/NDF is lower than 0.63 (extremum point) and dietary fat between 2.89% and 4.69% (extremum point), methane emissions may be achieved without losing lactation performance. Finally, given the difficulty of large-scale methane detection, we established the methane emission ANN prediction model (input layer: dietary fat, starch/NDF, DMI, milk fat proportion, milk protein yield, milk yield and their square; hidden layer: 12; output layer: methane; R^2 = 0.62; RMSE = 60.01, n = 292), which would provide predictive methane emission indicators for adjusting diet formulations, feeding strategies, and even breeding program in large-scale dairy farms.

Author contributions

Chenguang Zhang: conception and design, acquisition and analysis of data, original draft and editing. **Xingwei Jiang:** acquisition and interpretation of data. **Shengru Wu, Jun Zhang** and **Yue Wang:** reviewing. **Zongjun Li:** interpretation of data, reviewing and editing. **Junhu Yao:** reviewing and editing, funding acquisition, supervision.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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Appendix supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aninu.2024.02.004.

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