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Predicting the dynamics of enteric methane emissions based on intake kinetic patterns in dairy cows fed diets containing either wheat or corn



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ABSTRACT

The production of methane by the rumen microbiota is a complex biological process. When tackling the modelling of methane production, the modeller decides what complexity is needed to answer the scientific question for which the model is intended. Such a choice results in a diversity of possible models spanning both empirical and mechanistic approaches. Within the framework of precision livestock farming, simple dynamic models offer great advantages for integrating online data (e.g., feed intake) to predict individual methane emissions from cattle. Accordingly, we previously developed, with satisfactory results, a simple dynamic model that uses DM intake kinetics as a single predictor of methane emissions from finishing beef steers. The objective of the present work was to assess the capability of the previously developed model to predict the dynamic pattern of methane production from dairy cows fed a diet containing either wheat grain or corn grain. We showed that the simple dynamic model in its original form enables a description of the dynamics of individual methane emissions from dairy cows with an average determination coefficient (r^2) of 0.65 and an average concordance correlation coefficient of 0.81 and RMSE of 16% and 26% for the corn-based and wheat-based diets, respectively. Additionally, we performed a principal component analysis associating the parameters of the methane model with variables characterising the feeding behaviour of the cows. The results showed the effect of the diet type on the feeding behaviour of the animals. This impact was propagated on the dynamics of methane emissions. Interestingly, our model enabled us to determine that the differences in patterns of methane emissions between the diets result simply from the dependency of the methane yield and rate constant of methane eructation on the grain type.

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Implications

The integration of mathematical modelling with online data of key animal phenotypes is of great promise within the framework of precision livestock farming. This integration requires reliable and, ideally, simple models to facilitate the

implementation of monitoring algorithms and decision tools. The present work confirmed our previous studies showing that a simple dynamic model that uses DM intake kinetics as a single predictor of cattle methane emissions can produce satisfactory dynamic predictions of methane at the individual cow level.

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Specification table

Subject	Select one Section for your manuscript from the following list: <i>Livestock Farming Systems</i>
Type of data	List the type(s) of data the article describes. Simply delete from this list as appropriate: Table, script
How data were acquired	Data were acquired from respiration chambers and feed bins Data were filtered using R; statistical analysis was done in SAS and Minitab. A mathematical model was developed in Scilab.
Data format	Raw and filtered data
Parameters for data collection	The data come from a previously published article: Moate PJ, Williams SRO, Deighton MH, Hannah MC, Ribaux BE, Morris GL, Jacobs JL, Hill J and Wales WJ 2019. Effects of feeding wheat or corn and of rumen fistulation on milk production and methane emissions of dairy cows. <i>Animal Production Science</i> 59, 891–905.
Description of data collection	The original data come from an experiment conducted at the Department of Economic Development, Jobs, Transport and Resources, Ellinbank Centre, Victoria, Australia
Data source location	Institution: Agriculture Victoria Research City/Town/Region: Ellinbank, Victoria Country: Australia Latitude and longitude (and GPS coordinates, if possible) for collected samples/data: 38°14'37" S, 145°56'12" E
Data accessibility	Repository name: data.inrae Data identification number: https://doi.org/10.15454/CDUKML
Related research article	Moate PJ, Williams SRO, Deighton MH, Hannah MC, Ribaux BE, Morris GL, Jacobs JL, Hill J and Wales WJ 2019. Effects of feeding wheat or corn and of rumen fistulation on milk production and methane emissions of dairy cows. <i>Animal Production Science</i> 59, 891–905.

Introduction

Sustainable and environmentally acceptable production of meat, milk and wool from cattle, goats and sheep depends upon ruminal fermentation of ingested feed, and increasingly, upon reduced enteric methane emissions. Ruminal fermentation and methane production are dynamic processes mediated by interactions between the animal, its rumen microbiota and the diet. Mathematical models have long been used to advance our understanding of rumen function and to predict key animal phenotypes

(Dijkstra et al., 1992; Baldwin, 1995; Volpe et al., 2005). As with all models, the structure of a model and its level of aggregation (or detail) results from the subjective process of knowledge formalisation (Barnes, 1995; Tedeschi, 2019) that the modeller collates to describe the specific system. The subjective exercise of model construction can result in a diversity of models spanning different levels of complexity. Existing dynamic rumen models have represented in aggregated fashion the main drivers of ruminal fermentation and methane production (Mills et al., 2001; Ghimire et al., 2014; Huhtanen et al., 2015; van Lingen et al., 2019). The prediction capabilities of these models are yet to be improved (Offner and Sauvant, 2004; Bannink et al., 2016). Different authors have pointed out that to enhance the methane predictive capabilities of rumen models, improvements on the representation of key mechanisms are needed. Examples of opportunities for improvements in rumen models include a better representation of ruminal microbial metabolism (Ellis et al., 2008; Muñoz-Tamayo et al., 2016; Huws et al., 2018), the incorporation of thermodynamic drivers of fermentation (Janssen, 2010; van Lingen et al., 2019), and the incorporation of a mechanistic model to describe the dynamics of ruminal pH (Imamidoost and Cant, 2005; Bannink et al., 2016; Muñoz-Tamayo et al., 2016). Undertaking such improvements on the representation of biological phenomena in rumen models comes with the associated increase in model complexity and a rumen model that takes into account all of these features is still to be developed. In the meantime, with ruminant methane emissions becoming an issue of increasing concern, there is a role for simple dynamic models to help the prediction of methane production. In a previous work, we developed a simple dynamic model of methane emissions (Muñoz-Tamayo et al., 2019). The model was built using experimental data from finishing beef steers (Troy et al., 2015). The results of model performance were satisfactory, indicating the potential for exploiting the model in the context of precision farming. The objective of the present study was to assess the capability of the previously developed model to predict methane production kinetics from dairy cows fed a diet containing either wheat grain or corn grain.

Material and methods

Experimental data

The calibration and assessment of the models evaluated in this work were carried out using an experimental dataset obtained from the study of Moate et al. (2019). The experiment was carried out at the Agriculture Victoria Dairy Research Centre at Ellinbank, Victoria, Australia (38°14'37" S, 145°56'12" E). The study involved six rumen-fistulated Holstein dairy cows in late lactation fed either a wheat-based diet (**WHT**) or a corn-based diet (**CRN**) in a cross-over design. Animals were offered daily a total of 22.4 kg DM of a diet composed, on a DM basis, of 45.5% Lucerne hay, 8.9% cold-pressed canola, 0.5% minerals, 0.5% molasses, and 44.6% of either rolled wheat grain or rolled corn grain. Cows were individually offered feed twice daily at ~0630 h and 1530 h. Half of the daily feed allocation was offered at each feeding period. For each feeding period (0630–1530 h and 1530–0630 h), the concentrate (~7 kg wet mass) was offered to cows during the first 30 min while the cows were being milked. Then, the concentrate refusals were removed from the chamber and weighed. A second feed bin with Lucerne (~6 kg wet mass) was offered just after the removal of the concentrate bin in the chamber and stayed the remainder of the feeding period. The weight of the feed bins for Lucerne was registered every second by automatic scales (SmartScale 300; Gallagher, Hamilton, New Zealand). The feed bin with Lucerne refusals was removed just before the start of the next feeding period.

iod and the refused Lucerne was weighed manually. As the concentrate was consumed very quickly (*i.e.* in about 20–30 min during milking), we assumed a constant rate of DM intake (**DMI**) during the feeding of concentrate, calculated simply by the ratio between the concentrate consumed (in DM) and duration of the concentrate feeding interval. The files conc_XXXXYY.txt in the data repository <https://doi.org/10.15454/CDUKML> report the time interval of concentrate feeding and the weights of offered and refused concentrate for the animal XXX and the diet YYY. A full description of the experiment including the DM concentration and chemical composition of the feeds is given in Moate et al. (2019). The DM values of Lucerne and grains are given in the Scilab file DryMatterFeed.sci. The feeding regimen used in this experiment, *i.e.*, feeding the cows concentrate during milking followed by the forage part of the diet after milking, was chosen to replicate the feeding regimens commonly employed on dairy farms in Australia and New Zealand.

Feed consumption and methane emissions were simultaneously measured in an open-circuit respiration chamber for 2 days after a period of adaptation of 23 days. Methane measurements were reported every 12 min. The specifications of the respiration chamber facility are described in Grainger et al. (2007).

Filtering method for intake dynamics

DM intake is the primary driver of methane emission and thus an important input of methane models (Sauvant et al., 2011; Charmley et al., 2016). Accordingly, an accurate estimation of DMI is required to provide satisfactory methane predictions (Appuhamy et al., 2016).

The raw second by second data of feed intake (wet mass) obtained by Moate et al. (2019) are noisy and required ‘smoothing’ for our modelling purposes. We used an automatic algorithm developed on R (Blavy et al., 2020) to filter the raw data from the feed bins. Briefly, the algorithm constructs consecutive plateaus to filter the noise and remove outliers, secondly it detects feed distribution periods and finally it applies the longest decreasing sequence. The smoothed data (wet mass) were further adjusted to guarantee that the total amount of wet Lucerne consumed corresponded to the difference between the offered and refused Lucerne. We set the algorithm to export the smoothed wet mass values every minute. These values were further used to calculate the wet mass intake for time intervals of 4 min (files WMI_XX_X_YYY in the data repository). These values are further premultiplied by the percentage of DM of the feeds to calculate the DMI.

Mathematical modelling

We developed a filter model (Muñoz-Tamayo et al., 2019) that uses the dynamic pattern of DMI as the single predictor of the dynamic pattern of methane production. By applying a mass balance for methane production with a high level of aggregation of the biological processes that result in the formation of methane, we have the following simple model:

$$\frac{dx}{dt} = Y \cdot DMI - a \cdot x, x(0) = x_0 \quad (1)$$

where x (g) is the amount of enteric methane produced by the animal at a given time t . x_0 is the amount of methane at t_0 . The time derivative dx/dt describes how the amount of methane produced changes over time. The DMI (g DM·min⁻¹) represents the intake kinetics at t . The parameter Y (g CH₄/g DM⁻¹) is the methane yield that represents the grams of methane produced per gram of total DM (Lucerne plus grain) consumed by the animal, and the parameter a (min⁻¹) can be interpreted as the rate constant of methane eructation. The flux of methane emissions is given by the quantity

$z = a \cdot x$ (g·min⁻¹). The production of methane was measured in respiration chambers. As discussed in Muñoz-Tamayo et al. (2019), the dynamics of methane production measured in the chambers follows the dynamics of the flux of methane produced by the animal when the turnover rate of the chamber is optimally chosen. From Eq. (1), we obtain the time derivative of z :

$$\frac{dz}{dt} = a \cdot Y \cdot DMI - a \cdot z, z(0) = z_0 \quad (2)$$

where z_0 (g min⁻¹) is the initial flux of methane. We used the model in Eq. (2) to represent the dynamics of methane emissions. In addition to its simplicity, this model is structurally globally identifiable (that is, the model parameters are theoretically uniquely identifiable) which facilitates the estimation of its parameters (Muñoz-Tamayo et al., 2018). We used the backward differentiation method for the numerical solution of Eq. (2) with a step time of 4 min. The model was implemented in the open source software Scilab (<https://www.scilab.org/>) and the calibration was performed using the Nelder–Mead algorithm implemented in the `fminsearch` function. The yield factor Y was calculated directly from the experimental data while the parameter a and the initial condition z_0 were estimated from the calibration routine. The software R (<https://www.r-project.org/>) was used to plot the figures of the results.

Analysis of feeding behaviour

We analysed the intake kinetics after the filtering procedure by two methods. In the first approach, we used the method of Tolcamp et al. (1998) to split feeding behaviour pattern into bouts, also sometimes referred as meals, by using a log survivor function. In this study, the *bbi* (between bouts interval) or minimum time interval between meals was of 10 minutes. Then, we determined the number of bouts per feed period, the duration and size of each one. We also focused on the length and size of the first bout following feed offering to calculate the rate of intake of Lucerne during the first bout. In the second approach, we adjusted each kinetic of forage intake (*INTfo*) to the following exponential equation:

$$INTfo = INTfoMax \cdot (1 - \exp(-b \cdot t)) \quad (3)$$

where the parameter b is the fractional rate of satiety and *INTfoMax* is the asymptote of the forage intake (Baumont et al., 1990). The adjusted initial Intake Rate (*IRi*) was calculated from Eq. (3): $IRi = b \cdot INTfoMax$.

We further performed a statistical analysis on the feeding behaviour data with the `proc mixed` SAS procedure (version 9.4. SAS Institute, Inc, Cary, NC, USA). Data acquired from a given cow within a diet were considered as repeated means. The model included fixed effects of diet (wheat- or corn-based diet), cow and the interaction between diet type and cow. A principal component analysis (**PCA**) was also performed on the main behavioural data and parameters of the dynamic model of methane production in order to synthesise the links between feeding behaviour and methane production. We performed a PCA on 13 variables characterising the main behavioural data and those of the dynamic model of methane production in order to synthesise the links between feeding behaviour and methane production. For each parameter, the mean value of the four successive feed offerings per cow and per diet was calculated. As there were six cows in this experiment and as the experiment had a crossover design (two diets), the experiment provided 12 values per parameter. The 13 variables included in the PCA were as follows:

- (i) the methane yield (Y , g CH₄/g DMI)
- (ii) the eructation rate constant of methane (a , 1/min)
- (iii) the mean of the data of the four feed offerings per cow of total number of bouts (*NBOUT*)

- (iv) the total duration of the eating period (*DUREAT*, min)
- (v) the intake rate of forage (*QINTfo*, g/min)
- (vi) the duration of the first bout (*DUR_B1*, min)
- (vii) the proportion of intake during the first bout (*PrINT_B1*)
- (viii) the mean intake rate of this first bout (*IR_B1*, g/min)
- (ix) the mean of the data of the four feed offerings per cow of concentrate intake (*COint*, kg)
- (x) the satiety fractional rate (*b*, 1/min)
- (xi) the initial intake rate (*IRi*, g/min)
- (xii) the RMSE of Eq. (1) (RMSE, g)
- (xiii) the time to achieve the threshold of 2 kg of forage intake (Time2kg, min)

The PCA was performed using the Minitab software (version 18; Minitab LLC, State College, Pennsylvania, USA).

Results

The experimental data and the scripts of the model are available in the following link <https://doi.org/10.15454/CDUKML>. The Scilab scripts can be opened with any text editor.

Feeding behaviour

Fig. 1A shows the raw data (black diamonds) of Lucerne feed in the feed bin compared to the filtered data (continuous blue line) for one animal during 2 days. Thus, the blue line represents the smoothed data of the Lucerne feed remaining in the feed bin over the four consecutive feeding periods. It is observed in Fig. 1A that some raw data points are greater than the maximal amount of offered Lucerne (~6 kg). These data reflect the interaction of the animal with the feed bin resulting in aberrant data that must be removed for the modelling and also for feed intake analysis. Fig. 1B shows the dynamics of DMI calculated from the filtered data of feed consumption of Lucerne. The figure also shows the DMI for the concentrate.

The characteristics of the feeding behaviour associated with consumption of Lucerne hay during a feeding period are shown in Table 1. Cows fed the CRN diet ate on average, 4.94 kg DM of Lucerne hay per feeding period (i.e., 9.88 kg DM/d) while the cows offered the WHT diet ate 4.65 kg DM of Lucerne hay per feeding period (i.e., 9.3 kg DM per day) and these intakes of Lucerne hay were not different between diets ($P = 0.24$). When comparing CRN to WHT, the cows fed the CRN spent less time eating Lucerne

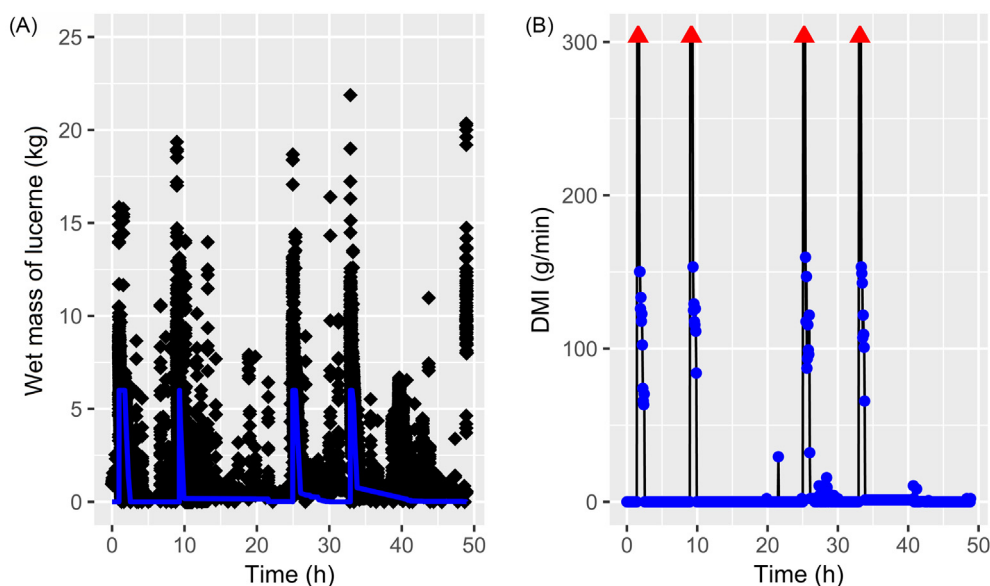


Fig. 1. Example of intake of a single cow. (A) Raw records (•) of wet mass of Lucerne in feed bins compared to the smooth data generated by the filtering algorithm (solid blue line) developed by Blavy et al. (2020). (B) Dry matter intake (DMI) of Lucerne (blue circles) calculated using the filtered data and DMI of concentrate (red triangles). For each feeding period, the concentrate was offered to cows during the first 30 min. Then, the concentrate refusals were removed from the chamber and weighted. As the concentrate was consumed very quickly, we assumed a constant DMI during the feeding of concentrate, calculated simply by the ratio between the concentrate consumed (in DM) and the duration of feeding interval. After removal of the concentrate feed bin in the chamber, a second feed bin with Lucerne was offered. The weight of the feed bins for Lucerne was registered every second in automatic scales. The wet mass records were further filtered and used to calculate the DMI every 4 min.

Table 1
Characteristics of the feeding behaviour of cows associated with consumption of Lucerne hay during a feed offering period.

Variable	CRN [†]	WHT [†]	P values			Mean SE
			Diet	Cow	Diet* [†] Cow	
Intake of Lucerne (kg DM)	4.94	4.65	0.24	0.74	0.73	0.023
Duration eating period (min)	81 ^a	120 ^b	<0.001	<0.001	0.01	5.91
Number of bouts	1.63 ^a	4.04 ^b	<0.001	0.01	0.001	0.499
Duration first bout (min)	78.0	86.4	0.08	<0.001	0.01	2.032
Intake first bout (kg DM)	4.90 ^a	4.02 ^b	<0.001	0.03	0.01	0.074
Intake rate first bout (g/min)	72.1 ^a	47.2 ^b	<0.001	<0.001	<0.001	1.52
Proportion of intake during the first bout	0.999	0.875	0.35	0.57	0.56	0.016

^{a-b} Values within a row with different superscripts differ significantly at $P < 0.05$.

[†] CRN: corn diet. WHT: wheat diet.

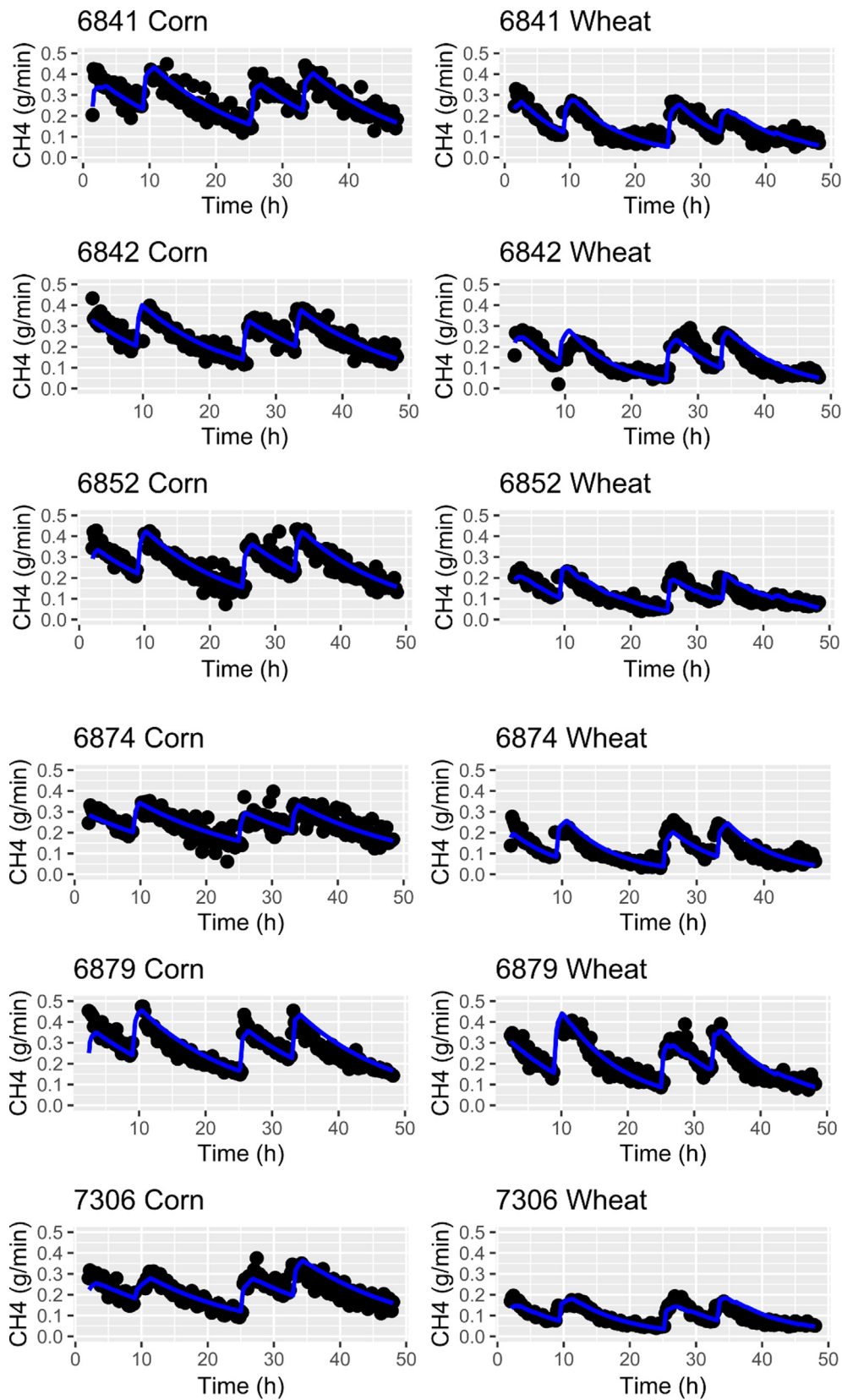


Fig. 2. Dynamics of methane emissions from cows fed either CRN or WHT diets. Experimental data of methane emission (•) are compared against predicted emissions given by the filter model (solid blue line). CRN: corn diet. WHT: wheat diet.

hay, and had a smaller number of eating bouts (Table 1). The main response difference between the diets relates to the first bout: three cows made a single bout of eating Lucerne hay after each feed offering on the CRN diet, and out of the 24 data recorded (six cows and four feed offerings per cow and diet), 17 corresponded to a unique bout. With the WHT diet, there were only four data with a single bout during which all or most of the Lucerne hay was consumed. The duration of the first bout tended to be shorter with the CRN diet compared to the WHT diet, but the Lucerne intake rate during the first bout was greater for the CRN diet than for the WHT diet. The cow effect was significant, except for the intake and the proportion eaten during the first bout. The interaction between the cow and diet was significant except for the total intake.

When the dataset containing the 48 kinetics of forage intake was used to predict *IRi*, the regression for *IRi* adjusting the data within cows was as follows:

$$IRi = 155.1 - 28.8[1 \text{ for WHT or } 0 \text{ for CRN}] - 17.3[\text{number of the successive feed offerings (from 1 to 4)}], (n = 48, RMSE = 45.2 \text{ g/min}) \tag{4}$$

All the effects were highly significant including the individual cow effect.

For the parameter *b*, we obtained the following regression:

$$b = 0.026 - 0.0101[1 \text{ for WHT or } 0 \text{ for CRN}] - 0.0029[\text{number of the successive feed offerings (from 1 to 4)}], (n = 48, RMSE = 0.007 \text{ min}^{-1}) \tag{5}$$

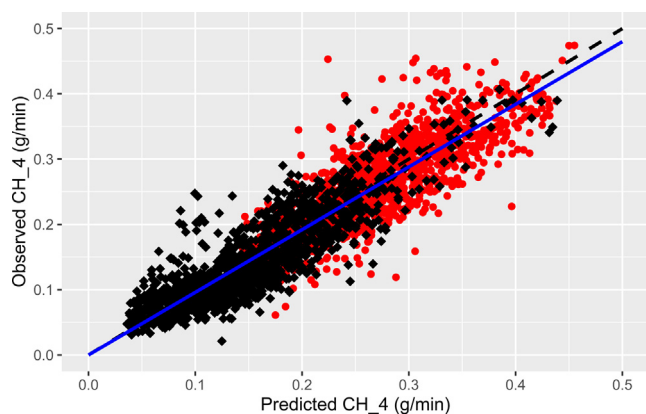


Fig. 3. Observed methane emissions of cows vs predicted methane by the filter model for WHT (●) and CRN (●). The dashed black line is the isocline. The solid blue line is the regression line. CRN: corn diet. WHT: wheat diet.

Table 2

Parameter estimates of the filter model and statistical indicators.

Cow	CRN [†]							WHT [†]						
	Y g CH ₄ /g DM ⁻¹	a 10 ³ min ⁻¹	z ₀ g CH ₄ min ⁻¹	r ²	CCC [*]	RMSE	CV _{RMSE} ^{**}	Y g CH ₄ /g DM ⁻¹	a · 10 ³ min ⁻¹	z ₀ g CH ₄ min ⁻¹	r ²	CCC [*]	RMSE	CV _{RMSE} ^{**}
6841	0.019	1.19	0.14	0.71	0.84	0.040	14	0.012	2.10	0.082	0.71	0.85	0.034	23
6842	0.017	1.17	0.15	0.71	0.84	0.038	16	0.011	2.24	0.076	0.68	0.83	0.040	28
6852	0.018	1.15	0.17	0.71	0.84	0.041	15	0.009	2.35	0.076	0.60	0.79	0.032	26
6874	0.016	0.85	0.16	0.59	0.75	0.037	15	0.008	2.28	0.039	0.58	0.78	0.039	32
6879	0.020	1.16	0.20	0.61	0.79	0.050	18	0.016	1.85	0.13	0.79	0.89	0.040	19
7306	0.016	1.03	0.18	0.60	0.77	0.040	18	0.007	2.02	0.078	0.61	0.80	0.026	26
Mean	0.018	1.09	0.17	0.65	0.80	0.041	16	0.010	2.14	0.080	0.66	0.82	0.035	26

[†] CRN: corn diet. WHT: wheat diet.

^{*} CCC: concordance correlation coefficient.

^{**} CV_{RMSE}: CV of the RMSE (%).

All the effects were highly significant including the individual cow effect.

Response of the filter model

Fig. 2 displays the response of the calibrated filter model for the six cows offered either CRN or WHT. The model satisfactorily captured the dynamics of methane flux. Fig. 3 shows all the experimental data against the predicted output of the filter model. As observed, methane emissions (g/min) by cows offered CRN are greater than the emissions by cows offered WHT. The regression line has a slope of 0.96. The intercept was not significantly different from zero (*P* > 0.05). The overall coefficient of determination is 0.84.

Table 2 shows the results of the calibration of the filter model and classical statistical indicators. Fig. 4 shows the boxplots for the parameter estimates of the filter model. For the CRN diet, the average values of the estimates were *Y* = 0.018 and *a* = 1.09 × 10⁻³. For the WHT, the average values of the estimates were *Y* = 0.010 and *a* = 2.14 × 10⁻³. For the model parameters, we did a decision test for the null hypothesis that the estimates for CRN and WHT have equal means using the t-test2 function of Matlab[®]. For both parameters, the null hypothesis was rejected at 5%

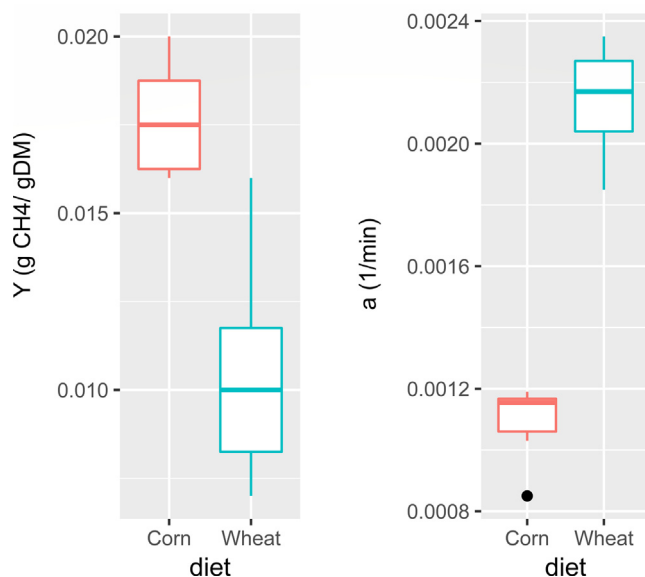


Fig. 4. Boxplot of the estimated parameters of the filter model.

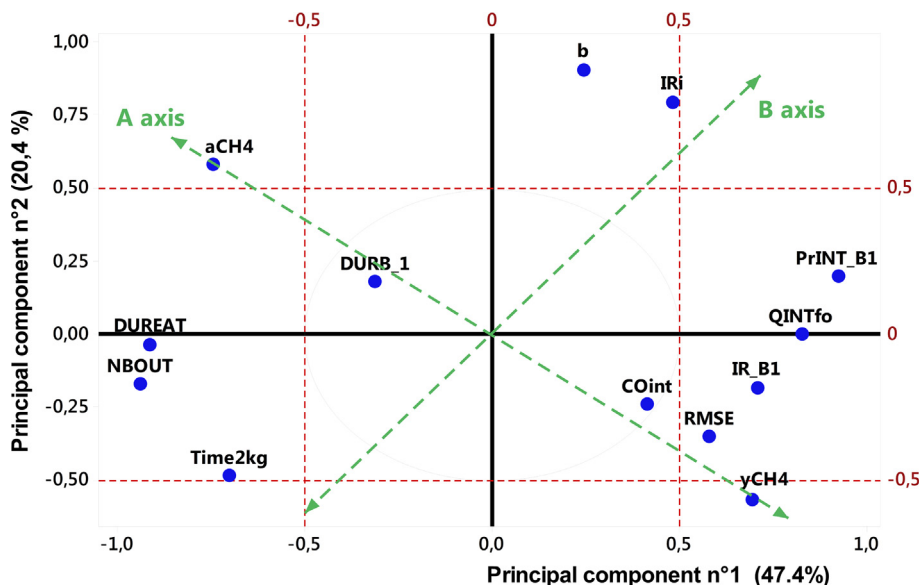


Fig. 5. Principal components 1 and 2 for feeding behaviour and methane production variables of cows.

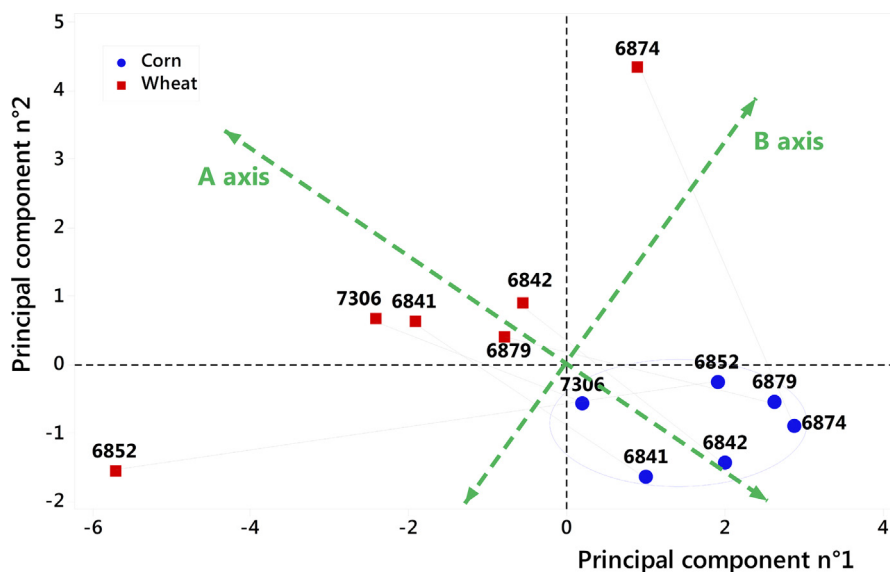


Fig. 6. Positions of the cows × diets in the principal components 1 and 2.

significance level. The parameter *a* was lower for CRN than WHT. The average methane yield of cows when the WHT diet was offered was 58% of the value of the methane yield of cows when the CRN diet was offered. Table 2 also shows the estimated initial flux of methane z_0 . The average z_0 was greater when the CRN diet was offered compared with when the WHT diet was offered.

Link between diet, feeding behaviour and methane production

Fig. 5 presents the correlations between the 13 variables and the first two principal components. Fig. 6 shows the position of the cows in the two first principal components. On the first principal component, which explained the majority of data variations (47.4%), we observe, in Fig. 5, a negative (inverse) correlation between two groups of variables related to the intake of Lucerne and methane production. The first group of variables includes forage intake, proportion of intake during the first bout, adjusted initial intake rate and intake rate in the first bout and methane yield.

The second group of variables includes the number of bouts, the duration of eating, the time to achieve 2 kg of eaten forage and the eructation rate constant of methane. The negatively correlated variables are positioned on opposite sides of the plot origin (opposed quadrants). Thus, the PC n°1 represents the forage intake which is closely and positively linked with the initial value of intake rate. Fig. 6 shows that the CRN is eaten in higher quantity with a higher initial IR than the WHT. This difference is significant on the PC n°1 ($P < 0.017$, RMSE = 1.57). Moreover, the dispersion of data of wheat diets on this PCn°1 is much larger (SD = 2.42 vs 0.97).

The second principal component explained less variation (20.4%). It was mainly caused by a negative correlation between (1) the group of rate constants of methane eructation rates and satiety associated with adjusted initial IRi and (2) the methane yield and the time to achieve 2 kg of forage intake (Fig. 5). Thus, beyond effects observed above on the PC n°1, a part of the variance of methane yield and eructation rate constant is linked with high rates of methane eructation and intake kinetics. Fig. 6 shows that

this component is mainly due to an extreme value of one cow (no. 6874) offered the WHT diet. The effect of diet is at the limit of significance on this PC n°2 and, as for the PC n°1, dispersion of data of the WHT diet was larger than the dispersion for the CRN diet (SD = 1.88 vs 0.75).

Figs. 5 and 6 show that the major discrimination between the two diets appeared along a diagonal line (A axis) that reflects the close and negative correlation between methane yield and eructation rate. On this A axis, large values of methane yield were associated with greater intake of concentrate and of forage, particularly during the first bout. Fig. 6 shows also the B axis, orthogonal to A, which is the axis of major discrimination between cows eating wheat, particularly the cows no. 6852 and 6874. The values of the variables for the PCA analysis are in the following link: <https://doi.org/10.15454/CDUKML>.

Author's point of view

Feeding behaviour and its link with methane production

The analysis of feeding behaviour described here should be taken with caution as the cows were not fed ad libitum. Nevertheless, results are in agreement with previous studies. When offered the CRN diet, cows ate almost all their Lucerne allowance during the first feeding bout just after the feed was offered. This suggests that the CRN imposed limited physiological or physical regulation on intake of this diet (Baile and Della-Fera, 1981). With the WHT diet, intake rate was smaller and cows spent more time eating and had more eating bouts. This between-diets difference has also been observed by Fulton et al. (1979) when steers received more than 50% of their diet as wheat, and they had a low rate of feed intake immediately after feed offering and did not compensate thereafter. As observed over the whole dataset, the intake rate during the first bout was greater with the CRN diet, because the cows ate more in a shorter duration, resulting in a greater total intake of concentrate intake compared to the total concentrate intake on the WHT diet. An important difference between diets relates to the different types of starch within wheat and corn grains. The starch in wheat is more quickly fermented within the rumen than corn starch and this may result in sub-clinical acidosis in cows offered wheat-based diets (Moate et al., 2019). In this experiment, the nadir in ruminal pH with the WHT diet was approximately 5.4 while for the CRN diet, it was approximately 5.8 (Moate et al., 2019). With the WHT diet, cows tended to counteract the excessive flow of nutrients with this highly degradable starch (de Smet et al., 1995) by decreasing their intake rate, especially during the first bout. These aspects could explain why late stage corn silage with high DM concentration with slowly degradable starch has a smaller fill effect than early stage corn silage having a low DM concentration (Nozière et al., 2018). The cow effect was highly significant with almost all parameters and is in agreement with the previous work of Moate et al. (2018), which pointed out that some cows do not adapt to the WHT diet. We speculate that the negative correlation between intake and duration (or number of bouts) is a consequence of the feeding behaviour of cows that decreased their intake rate in response to sub-clinical acidosis when they consumed the WHT diet. The methane emission even expressed on a DM basis was greater for the CRN diet that was eaten in a greater quantity. The observed between-cow differences are in agreement with previous publications (Cabezas-Garcia et al., 2017).

Analysis of the filter model

This work confirmed our previous results on the satisfactory performance of the dynamic model to predict the dynamic pattern

of methane emissions from the intake kinetic pattern (Muñoz-Tamayo et al., 2019).

In our previous work, when testing for a difference in the model parameters in diets with different forage to concentrate ratios, we found that the rate constant of eructation was not significantly different between diets. Accordingly, we concluded that the diet treatment did not affect the rate at which methane is released (Muñoz-Tamayo et al., 2019). Although we should be cautious on developing a hypothesis on the basis of the limited data analysed in the present work, our model captured effects of the diet on the rate constant of eructation. Altogether, these findings suggest that the different action mechanisms of dietary strategies for methane mitigation may be captured by the methane yield and the rate constant of eructation. Consequently, we consider it is important that these two parameters be taken into account when evaluating and designing methane mitigation strategies.

Conclusions

We have shown that although the biological process involved in the production of methane by cattle is complex, a simple dynamic model that uses as single predictor, the pattern of DMI, provides satisfactory results in predicting the individual dynamic patterns of methane production. The type of diet affects the feeding behaviour of the animals. This impact is propagated onto the dynamics of methane emissions, which are captured adequately by our model. Despite the simple structure of the model, its parameters are biologically meaningful which facilitates interpretation and analysis. In particular, we showed that the diet not only affects methane yield but also the rate constant of gas eructation. These two parameters should be taken into consideration when evaluating diets for methane mitigation.

Ethics approval

Original data procurement ethical review is described in Moate et al. (2019).

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Author contributions

SROW and PJM produced the experimental data of the study. PB, BR and RMT filtered the data of feed intake kinetics. BR and RMT developed the code for calibration of the model of methane emissions. SGR and DS did the analysis of feeding behaviour. RMT, PJM, SGR and DS drafted the paper. All authors read and approved the final manuscript.

Declaration of interest

The authors declare that they have no competing interests.

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References

- Appuhamy, J.A.D.R.N., France, J., Kebreab, E., 2016. Models for predicting enteric methane emissions from dairy cows in North America, Europe, and Australia and New Zealand. *Global Change Biology* 22, 3039–3056.
- Baile, C.A., Della-Fera, M.A., 1981. Nature of hunger and satiety control systems in ruminants. *Journal of Dairy Science* 64, 1140–1152.
- Baldwin, R.L., 1995. Modeling ruminant digestion and metabolism. Chapman and Hall, London, UK.
- Bannink, A., van Lingen, H.J., Ellis, J.L., France, J., Dijkstra, J., 2016. The contribution of mathematical modeling to understanding dynamic aspects of rumen metabolism. *Frontiers in Microbiology* 7, 1820.
- Barnes, C.J., 1995. The art of catchment modeling: What is a good model? *Environment International* 21, 747–751.
- Baumont, R., Segulier, N., Dulphy, J.P., 1990. Rumen fill, forage palatability and alimentary behaviour in sheep. *The Journal of Agricultural Science* 115, 277–284.
- Blavy, P., Dhumez, O., Nielsen, B., Muñoz-Tamayo, R., Friggens, N., Giger-Reverdin, S., 2020. A filtering algorithm for accurate determination of feed intake dynamics. <https://hal.archives-ouvertes.fr/hal-02959928>.
- Cabezas-García, E.H., Krizsan, S.J., Shingfield, K.J., Huhtanen, P., 2017. Between-cow variation in digestion and rumen fermentation variables associated with methane production. *Journal of Dairy Science* 100, 4409–4424.
- Charmley, E., Williams, S.R.O., Moate, P.J., Hegarty, R.S., Herd, R.M., Oddy, V.H., Reyenga, P., Staunton, K.M., Anderson, A., Hannah, M.C., 2016. A universal equation to predict methane production of forage-fed cattle in Australia. *Animal Production Science* 56, 169–180.
- Dijkstra, J., Neal, H.D., Beaver, D.E., France, J., 1992. Simulation of nutrient digestion, absorption and outflow in the rumen: model description. *Journal of Nutrition* 122, 2239–2256.
- Ellis, J.L., Dijkstra, J., Kebreab, E., Bannink, A., Odongo, N.E., McBRIDE, B.W., France, J., 2008. Aspects of rumen microbiology central to mechanistic modelling of methane production in cattle. *The Journal of Agricultural Science* 146, 213–233.
- Fulton, W.R., Klopfenstein, T.J., Britton, R.A., 1979. Adaptation to High Concentrate Diets by Beef Cattle. I. Adaptation to Corn and Wheat Diets. *Journal of Animal Science* 49, 775–784.
- Ghimire, S., Gregorini, P., Hanigan, M.D., 2014. Evaluation of predictions of volatile fatty acid production rates by the Molly cow model. *Journal of Dairy Science* 97, 354–362.
- Grainger, C., Clarke, T., McGinn, S.M., Auld, M.J., Beauchemin, K.A., Hannah, M.C., Waghorn, G.C., Clark, H., Eckard, R.J., 2007. Methane emissions from dairy cows measured using the sulfur hexafluoride (SF₆) tracer and chamber techniques. *Journal of Dairy Science*.
- Huhtanen, P., Ramin, M., Udén, P., 2015. Nordic dairy cow model Karoline in predicting methane emissions: 1. Model description and sensitivity analysis. *Livestock Science* 178, 71–80.
- Huws, S.A., Creevey, C.J., Oyama, L.B., Mizrahi, I., Denman, S.E., Popova, M., Muñoz-Tamayo, R., Forano, E., Waters, S.M., Hess, M., Tapio, I., Smidt, H., Krizsan, S.J., Yáñez-Ruiz, D.R., Belanche, A., Guan, L., Gruninger, R.J., McAllister, T.A., Newbold, C.J., Roehe, R., Dewhurst, R.J., Snelling, T.J., Watson, M., Suen, G., Hart, E.H., Kingston-Smith, A.H., Scollan, N.D., do Prado, R.M., Pilau, E.J., Mantovani, H.C., Attwood, G.T., Edwards, J.E., McEwan, N.R., Morrisson, S., Mayorga, O.L., Elliott, C., Morgavi, D.P., 2018. Addressing global ruminant agricultural challenges through understanding the rumen microbiome: past, present, and future. *Frontiers in Microbiology* 9, 2161.
- Imamidoost, R., Cant, J.P., 2005. Non-steady-state modeling of effects of timing and level of concentrate supplementation on ruminal pH and forage intake in high-producing, grazing ewes. *Journal of Animal Science* 83, 1102–1115.
- Janssen, P.H., 2010. Influence of hydrogen on rumen methane formation and fermentation balances through microbial growth kinetics and fermentation thermodynamics. *Animal Feed Science and Technology* 160, 1–22.
- van Lingen, H.J., Fadel, J.G., Moraes, L.E., Bannink, A., Dijkstra, J., 2019. Bayesian mechanistic modeling of thermodynamically controlled volatile fatty acid, hydrogen and methane production in the bovine rumen. *Journal of Theoretical Biology* 480, 150–165.
- Mills, J.A., Dijkstra, J., Bannink, A., Cammell, S.B., Kebreab, E., France, J., 2001. A mechanistic model of whole-tract digestion and methanogenesis in the lactating dairy cow: model development, evaluation, and application. *Journal of Animal Science* 79, 1584–1597.
- Moate, P.J., Jacobs, J.L., Hannah, M.C., Morris, G.L., Beauchemin, K.A., Hess, P.S.A., Eckard, R.J., Liu, Z., Rochfort, S., Wales, W.J., Williams, S.R.O., 2018. Adaptation responses in milk fat yield and methane emissions of dairy cows when wheat was included in their diet for 16 weeks. *Journal of Dairy Science* 101, 7117–7132.
- Moate, P.J., Williams, S.R.O., Deighton, M.H., Hannah, M.C., Ribaux, B.E., Morris, G.L., Jacobs, J.L., Hill, J., Wales, W.J., 2019. Effects of feeding wheat or corn and of rumen fistulation on milk production and methane emissions of dairy cows. *Animal Production Science* 59, 891–905.
- Muñoz-Tamayo, R., Giger-Reverdin, S., Sauvant, D., 2016. Mechanistic modelling of in vitro fermentation by rumen microbiota. *Animal Feed Science and Technology* 220, 1–21.
- Muñoz-Tamayo, R., Puillet, L., Daniel, J.B., Sauvant, D., Martin, O., Taghipoor, M., Blavy, P., 2018. Review: To be or not to be an identifiable model. Is this a relevant question in animal science modelling? *Animal* 12, 701–712.
- Muñoz-Tamayo, R., Ramirez Agudelo, J.F., Dewhurst, R.J., Miller, G., Vernon, T., Kettle, H., 2019. A parsimonious software sensor for estimating the individual dynamic pattern of methane emissions from cattle. *Animal* 13, 1180–1187.
- Nozière, P., Sauvant, D., Delaby, L. (Eds.), 2018. INRA feeding system for ruminants. Wageningen Academic Publishers, Wageningen, The Netherlands.
- Offner, A., Sauvant, D., 2004. Comparative evaluation of the Molly, CNCPS, and LES rumen models. *Animal Feed Science and Technology* 112, 107–130.
- Sauvant, D., Giger-Reverdin, S., Serment, A., Broudiscou, L., 2011. Influences of diet and rumen fermentation on methane production by ruminants. *Inra Productions Animales* 24, 433–446.
- de Smet, A.M., de Boever, J.L., de Brabander, D.L., Vanacker, J.M., Boucqué, C.V., 1995. Investigation of dry matter degradation and acidotic effect of some feedstuffs by means of in sacco and in vitro incubations. *Animal Feed Science and Technology* 51, 297–315.
- Tedeschi, L.O., 2019. Mathematical modeling in ruminant nutrition: approaches and paradigms, extant models, and thoughts for upcoming predictive analytics. *Journal of Animal Science* 97, 1921–1944.
- Tolkamp, B.J., Allcroft, D.J., Austin, E.J., Nielsen, B.L., Kyriazakis, I., 1998. Satiety splits feeding behaviour into bouts. *Journal of Theoretical Biology* 194, 235–250.
- Troy, S.M., Duthie, C.A., Hyslop, J.J., Roehe, R., Ross, D.W., Wallace, R.J., Waterhouse, A., Rooke, J.A., 2015. Effectiveness of nitrate addition and increased oil content as methane mitigation strategies for beef cattle fed two contrasting basal diets. *Journal of Animal Science* 93, 1815–1823.
- Volpe, V., Boston, R.C., Susmel, P., Moate, P.J., France, J., Dijkstra, J., 2005. The use of WinSAAM for modelling complex ruminal metabolism. In: Hargrove, J.L., Berdanier, C.D. (Eds.), *Mathematical modeling in nutrition and toxicology*. Mathematical Biology Press, Athens, Georgia, USA, pp. 111–139.