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Prediction of enteric methane emissions by sheep using an intercontinental database

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ABSTRACT

Enteric methane (CH_4) emissions from sheep contribute to global greenhouse gas emissions from livestock. However, as already available for dairy and beef cattle, empirical models are needed to predict CH_4 emissions from sheep for accounting purposes. The objectives of this study were to: 1) collate an intercontinental database of enteric CH_4 emissions from individual sheep; 2) identify the key variables for predicting enteric sheep CH_4 absolute production (g/d per animal) and yield [g/kg dry matter intake (DMI)] and their respective relationships; and 3) develop and cross-validate global equations as well as the potential need for age-, diet-, or climatic region-specific equations. The refined intercontinental database included 2,135 individual animal data from 13 countries. Linear CH_4 prediction models were developed by incrementally adding variables. A universal CH_4 production equation using only DMI led to a root mean square prediction error (RMSPE, % of observed mean) of 25.4% and an RMSPE-standard deviation ratio (RSR) of 0.69. Universal equations that, in addition to DMI, also included body weight (DMI + BW), and organic matter digestibility (DMI + OMD + BW) improved the prediction performance further (RSR, 0.62 and 0.60), whereas diet composition variables had negligible effects. These universal equations had lower prediction error than the extant IPCC 2019 equations. Developing age-specific models for adult sheep (>1-year-old) including DMI alone (RSR = 0.66) or in combination with rumen propionate molar proportion (for research of more refined purposes) substantially improved prediction performance (RSR = 0.57) on a smaller dataset. On the contrary, for young sheep (<1-year-old), the universal models could be applied, instead of age-specific models, if DMI and BW were included. Universal models showed similar prediction performances to the diet- and region-specific models. However, optimal prediction equations led to different regression coefficients (i.e. intercepts and slopes) for universal, age-specific, diet-specific, and region-specific models with predictive implications. Equations for CH_4 yield led to low prediction performances, with DMI being negatively and BW and OMD positively correlated with CH_4 yield. In conclusion, predicting sheep CH_4 production requires information on DMI and prediction accuracy will improve national and global inventories if separate equations for young and adult sheep are used with the additional variables BW, OMD and rumen propionate proportion. Appropriate universal equations can be used to predict CH_4 production from sheep across different diets and climatic conditions.

1. Introduction

Continued increases in emissions of greenhouse gases (GHG) have a substantial impact on climate change, which represents a threat to global food security. We, as a society, are challenged to mitigate GHG emissions to achieve the commitments under the Paris Agreement. Livestock production generates 7.1 Gt of CO_2 equivalents per year representing approximately 14.5% of the global anthropogenic GHG emissions (Gerber et al., 2013). Enteric CH_4 is a natural product derived from microbial fermentation of feeds, representing a major fraction of the livestock CH_4 production, as well as a loss of 2–12% of the gross energy (GE) intake in ruminants (Niu et al., 2018; IPCC, 2019). The global sheep population of 1.2 billion produces approximately 6.4% total of the total enteric CH_4 from livestock (Patra, 2014a) and is the third most-emitting ruminant species after cattle and buffaloes (FAOSTAT, 2020). The sheep sector contributes to many of the Sustainable Development Goals (SDG) described by the United Nations. Therefore, it is widely accepted that sheep production should remain at the current level (Belanche et al., 2021). However, the projected increases in global meat (+73%) and milk demand (+58%) make it difficult to achieve the enteric CH_4 mitigation goals (of up to −47%) between 2010 and 2050 (Beauchemin et al., 2020). Attempts to reduce enteric CH_4 emissions will involve the implementation of mitigation strategies without impairing ruminant productivity, health and well-being that can help to meet the 1.5 °C target by 2030 but not 2050 (Arndt et al., 2022). However, to determine the environmental impact of ruminant agriculture and the potential effectiveness of mitigation strategies, the enteric CH_4 emissions across all ruminant species and systems need to be quantified accurately.

Several empirical models have been developed using databases from different studies to estimate enteric CH_4 emissions and understand the diet composition factors that affect rumen fermentation and methanogenesis in cattle (Mills et al., 2003; Kebreab et al., 2008) and buffalo (Patra, 2014b). Recently, diet- and region-specific equations for dairy (Niu et al., 2018) and beef cattle systems (van Lingen et al., 2019) have been published using large intercontinental databases. For sheep, however, similar resource of CH_4 emission data covering different regions and systems has not been developed to date. The Intergovernmental Panel on Climate Change (IPCC) has developed methodologies to estimate enteric CH_4 emissions based on the so called CH_4 emission factors (Y_m), which represent the proportion of gross energy intake (GEI) that is emitted as CH_4 energy. The latest IPCC guidelines (IPCC, 2019) suggest using a default Y_m value of 6.7% for all categories of sheep and diets, with values of 7.0% and 6.5% being more appropriate when the average dry matter intake (DMI) is < 0.6 or >0.8 kg/d, respectively. However, this value was calculated based on treatment means derived mostly from measurements made in New Zealand using high-quality forage diets (Swainson et al., 2018). Moreover, the Y_m-based models do not directly capture variations in CH_4 emissions determined by changes in diet composition, rumen fermentation pattern, or type of animal (e.g., young vs. adult sheep), which limit their usefulness (Moraes et al., 2014) and can result in inaccuracies in the preparation of national GHG inventories or cost-benefits assessment of mitigation strategies.

Given the wide diversity among sheep production systems varying in type of diets, rearing systems and breeds (Pulina et al., 2018), there is a need to develop equations that can predict enteric CH_4 emissions across all those systems. To address this issue, there have been attempts to use or re-adapt equations derived from cattle for sheep (Vetharaniam et al., 2015), but the differences in the type of diets, gut physiology (e.g., rumen retention time, feeding level and microbiota) and feeding behavior have limited their utility. Sheep-specific models have been developed using relatively small (Pelchen and Peters, 1998; Patra et al., 2016) or country-specific databases (Muetzel and Clark, 2015; Swainson et al., 2018) based on individual animal or treatment mean data. However, the relatively small number of observations, diet types and geographical regions have limited the use of these models universally. Some of these studies (Van Lingen et al., 2019) have shown that more complex models including diet composition and sheep body weight (BW), in addition to feed intake, could increase the predictive accuracy of enteric CH_4 emissions. Thus, models with different levels of complexity and/or specific models for different animal age-categories, diets or climatic regions need to be developed and evaluated. Moreover, the trade-off between on-farm availability of input data and prediction accuracy of the models must be carefully considered to maximize its value for potential users with access to different levels of information (e.g., farmers, extension services staff, researchers, environmental agencies, policy makers and national and global inventories).

Therefore, the objectives of the present study were to: 1) collate an intercontinental database of enteric CH_4 emissions from individual sheep; 2) determine the key variables (including DMI, diet composition, rumen fermentation variables, feed digestibility, and BW) for predicting sheep enteric CH_4 absolute production (g/d per animal) and yield (g/kg DMI); and 3) develop and evaluate universal models as well age-specific, diet-specific or climatic region-specific models as needed.

2. Material and methods

2.1. Database processing

The "GLOBAL NETWORK" (Global Network for the Development and Maintenance of Nutrition-Related Strategies for Mitigation of Methane and Nitrous Oxide Emissions from Ruminant Livestock; www.globalresearchalliance.org) is an international collaborative initiative in which animal scientists with potential access to *in vivo* CH_4 measurements from sheep were invited to provide data. The initial database consisted of 2,973 individual CH_4 records from 71 published and unpublished experiments conducted between 2003 and 2018 in research institutions across 13 countries. A detailed description of the initial database is provided as Supplementary Material (Supplementary Table S1). The majority of the studies in the database investigated the impact of diet composition or feeding level on enteric CH_4 production, rumen fermentation, feed efficiency, and productivity. However, some studies tested the effect of feed additives or plants with well-documented modulatory effects on rumen function or CH_4 production. For the studies that used CH_4 inhibitors (e.g., nitrate, 2-bromo-ethylsulfonate, 3-nitrooxy-propionate, 3-nitrooxy-propanol and di-allyl-disulphide) and feed additives that potentially modify the rumen microbiota and can indirectly impact CH_4 production (e.g., essential oils, garlic oil, pequi oil, cashew nut shell extract, saponins extracts, tannins extracts, plants rich in tannins, probiotics and protozoal removal), only the data of the non-supplemented control treatments were retained in the database to prevent potential bias. Moreover, eight records with missing CH_4 or DMI values were excluded to conform to the partially-refined database (n = 2,175).

Outliers were screened using the interquartile range (IQR) method (Zwilinger and Kokoska, 2000) as described by Niu et al. (2018). A factor of 1.5 for extremes was used in constructing boundaries to identify outliers for CH_4 yield and a factor of 2.5 for the independent variables. After this process, a refined database (summarized in Table 1) was obtained containing the information on CH_4 production, DMI, dietary concentrations of ash, CP, NDF, ADF, and the proportion of forage (For) on a DM basis. Some studies also reported dietary EE and GE concentrations (n = 965). In cases they were not reported but the feed ingredients and proportions in the diets were still provided, the EE content was calculated from published values (www.feedipedia.org) and the GE content was estimated according to the equation described by Weiss and Tebbe (2019):

$$\text{GE (MJ/kg DM)} = [\text{CP \%} \times 0.056 + \text{EE \%} \times 0.094 + (100 - \text{CP \%} - \text{EE \%} - \text{ash \%}) \times 0.042] \times 4.187$$

The refined database (n = 2,135, representing 70% of the initial database) contained individual animal data from 70 international studies from New Zealand (n = 647 from 22 experiments), Australia (n = 474 from 12 experiments), United Kingdom (n = 391 from 6 experiments), Brazil (n = 239 from 11 experiments), France (n = 132 from 5 experiments), Norway (n = 92 from 2 experiments), Switzerland (n = 90 from 6 experiments), Mexico (n = 32 from 1 experiment), Argentina (n = 13 from 1 experiment), Spain (n = 9 from 1 experiment), Peru (n = 8

Table 1
Summary statistics of all data included in the refined database and subsets of adult (>1-year-old) and young sheep (<1-year-old).

	All data (n = 2,135)				Adult sheep (n = 1,374)				Young sheep (n = 761)			
	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
Dry matter intake (kg/d)	1.01	0.22	2.74	0.36	1.05	0.32	2.74	0.36	0.94	0.22	2.13	0.34
GE intake (MJ/d)	17.8	3.88	48.8	6.23	18.4	5.64	48.8	6.32	16.6	3.88	36.7	5.89
Body weight (kg)	45.7	15.0	112	14.3	52.1	19.5	112	12.7	34.1	15.0	75.0	8.80
Diet composition (% of DM)												
Crude protein	14.8	3.11	29.7	4.39	14.1	3.55	27.3	3.76	16.0	3.11	29.7	5.12
Ether extract	2.80	0.69	8.47	1.02	2.62	1.00	8.47	0.98	3.11	0.69	7.75	1.03
Ash	8.58	2.49	20.6	2.63	8.33	2.49	15.5	2.16	9.04	2.80	20.6	3.28
Neutral detergent fibre	51.1	15.2	80.5	9.69	52.1	26.9	80.5	9.04	49.5	15.2	77.1	10.6
Acid detergent fibre	27.5	8.17	47.4	5.48	28.2	13.4	47.4	5.22	26.2	8.17	41.4	5.70
GE (MJ/kg DM)	17.6	15.1	20.1	0.58	17.5	15.5	19.2	0.48	17.7	15.1	20.1	0.71
Forage (% of DM)	95.8	20.6	100	11.5	97.2	20.6	100	9.97	93.2	40.0	100	13.6
Rumen parameters												
Rumen pH	6.74	5.62	7.70	0.28	6.68	5.62	7.70	0.27	6.81	5.96	7.33	0.27
Ammonia-N (mmol/L)	11.3	1.15	63.6	10.1	12.4	1.18	63.6	11.9	10.2	1.15	54.5	7.65
Total VFA (mmol/L)	80.3	16.5	181	23.1	78.5	16.5	151	22.8	81.7	29.4	181	23.4
Acetate (%)	65.0	40.3	86.9	7.71	62.3	40.3	86.9	7.91	67.5	47.1	81.7	6.57
Propionate (%)	20.3	8.08	36.2	4.60	21.7	8.70	36.2	4.67	19.0	8.08	34.8	4.13
Butyrate (%)	10.4	0.49	25.4	3.94	11.6	0.49	25.4	4.45	9.36	2.59	24.8	3.01
Acetate to propionate ratio	3.46	1.23	9.99	1.30	3.12	1.23	9.99	1.30	3.79	1.51	9.75	1.22
OM digestibility (%)	65.7	35.1	93.5	10.6	64.0	44.8	93.5	8.78	69.5	35.1	90.8	13.3
Methane (CH_4) emissions												
CH_4 production (g/d)	19.7	3.57	57.1	7.29	21.3	4.62	57.1	7.22	17.0	3.57	44.8	6.58
CH_4 yield (g/kg DMI)	19.9	6.84	33.2	4.71	20.7	6.92	33.2	4.41	18.6	6.84	32.6	4.92
Y_m (% of GE intake)	6.33	2.11	10.8	1.51	6.59	2.17	10.5	1.41	5.86	2.11	10.8	1.56

GE = gross energy; VFA = volatile fatty acids; OM = organic matter; Y_m = CH_4 emission factor.

from 1 experiment), Egypt ($n = 6$ from 1 experiment) and Canada ($n = 2$ from 1 experiment). Enteric CH_4 emission data were obtained from respiration chambers (n = 1,762), SF_6 (n = 344) and the GreenFeed system (C-Lock Inc. South Dakota, USA, n = 29). Feed ingredients are described in Supplementary Material.

Universal prediction equations were developed using all the observations included in the refined database. Moreover, this database was divided into several subsets according to various criteria to develop category-specific prediction models. Specifically, based on the age of the animals and following the IPCC classification criteria (IPCC, 2006), the full database was divided into adult sheep (≥1-year-old, n = 1,374) and young sheep (<1-year-old, n = 761). The database was also split into a forage-diet (FD) subset (n = 1,797, ≥95% forage) and a mixed-diet (MD) subset (n = 338, from 20 to 95% forage). This forage-content threshold was chosen based on an analysis of different cut-offs as described below. To explore the impact of the type of climatic region on CH_4 production and yield, two subsets were considered according to the location and the Köppen climate classification based on seasonal precipitation and temperature patterns (Jagai et al., 2007): temperate climatic regions (mostly including temperate oceanic and humid continental climates) included studies from New Zealand, United Kingdom, Norway, Switzerland and Canada (n = 1,222); and warm climatic regions (mostly including the Mediterranean and Semi-Arid climates) included studies from Australia, Brazil, France (French West Indies), Mexico, Argentina, Spain, Peru and Egypt (n = 913). Average weight gain was only reported in five experiments (n = 176 observations). This limitation did not allow the development of sound equations for CH_4 intensity.

2.2. Model development

Mixed-effect models were developed to predict methane production (g/d) and yield (g/kg DMI) using the refined database as outlined by Van Lingen et al. (2019):

$$Y_{ij} = \beta_0 + \beta_1 X_{ij1} + \beta_2 X_{ij2} + \ldots + \beta_k X_{ijk} + S_i + \mathcal{E}_{ij}$$

Where Y_{ij} denotes the jth response variable of CH_4 production from the ith experiment; β_0 denotes the fixed effects of intercept; X_{ij1} to X_{ijk} denote the fixed effect of predictor variables and β_1 to β_k are the corresponding slopes; S_i denotes the random effect of the experiment, and $\mathcal{E}_{ij}$ denotes the residual error. All models were fitted using the lmer procedure (Bates et al., 2015) available through the lme4 package of R statistical language (R Core Team, 2021, version 4.1.0).

Model development was conducted using a sequential approach by incrementally adding different variables to develop models with increasing complexity. To obtain equations that depend on various predictor variables, 12 categories of CH_4 production models were developed, with seven using a fixed and five using a selected combination of variables. The fixed models predicted CH_4 production based on DMI only, GEI only, DMI + BW, DMI + OMD + BW, the IPCC_2006 equation (which proposed fixed Y_m values of 4.5% and 6.5% of GE intake for animals <1 and >1-year-old, respectively), the IPCC_2019_fix equation (Y_m = 6.7%), and the IPCC_2019_var (which proposed Y_m values of 7.0%, 6.7% and 6.5% for DMI <0.6, 0.6–0.8 and > 0.8 kg/d, respectively, regardless of the animal age). The models which were designed to select the best combination of variables were: the 'Diet' model, which could select among the variables DMI and dietary ash, CP, EE, NDF, ADF, For, and GE content; the 'Animal' model, which included the same variables as the Diet model plus BW; the 'Animal_no_DMI' model which included the same variables as the Animal model except for DMI; the 'Animal_VFA' model which included DMI, BW, and the rumen molar proportions of acetate, propionate and butyrate and the acetate to propionate ratio; and the 'Global' model which included all available variables described in the previous models. The entire refined database (n = 2,135) was used for model selection and subsequent model evaluation of certain universal models such as DMI, GEI, Diet and IPCC models, whereas the number of observations was reduced (due to missing data) to 1,810, 1,020 and 584 for universal models which included BW, OMD or VFA, respectively. Therefore, the highest possible number of observations was used for the development of each model. This approach maximized the data used for each equation but also made comparisons across models of different sizes more difficult.

Variables that potentially play a key role in predicting CH_4 production in the Diet, Animal, Animal_no_DMI, Animal_VFA, and Global models were selected using a multi-step selection approach as follows. Briefly, model selection started by evaluating the prediction performance of each variable followed by including complex combinations of the variables available. Only variables selected in an earlier step could be chosen for the next step based on a backward selection approach (van Lingen et al., 2019). The Bayesian information criterion (BIC) scores (James et al., 2014) were computed and the models with the lowest BIC values, which indicates the best trade-off between the goodness of fit and the model complexity, were used. The presence of multi-collinearity of fitted models was examined based on the variance inflation factor (Kutner et al., 2005). A stringent cut-off value of 3 was set to identify and exclude variables with potential multi-collinearity (e.g. DMI and GEI) from the models one at a time (Zuur et al., 2010).

2.3. Cross-validation and model evaluation

The predictive performance of the fitted CH_4 prediction models, including IPCC equations, was evaluated using the revised k-fold cross-validation method (James et al., 2014) applied to the same database used for model development with individual experiments considered a fold. This implied that each experiment was treated as a testing set and the CH_4 prediction performance was computed using the model that was fitted to the training set of all remaining experiments (Moraes et al., 2014). In order to evaluate the potential applicability of the models, including IPCC equations, across different ages, diets and climatic regions, the predictive performance of each model was also assessed on various subsets (adult *vs* young sheep, FD *vs* MD diets and temperate *vs* warm climatic regions). A combination of model evaluation metrics was used to assess model performance, including mean square prediction error (MSPE) as follows (Bibby and Toutenburg, 1977)

$$\text{MSPE} = \frac{\sum_{i=1}^{n} (O_i - P_i)^2}{n}$$

where O_i and P_i denoted the observed and predicted value of the response variable (CH_4) of the ith observation, respectively, and n indicates the number of observations in the database. The square root of the MSPE (RMSPE) was used to assess the overall model prediction error and was expressed as a percentage of observed CH_4 production or yield means in order to minimize the potential bias when comparing models developed from different databases. The MSPE was decomposed into mean bias (MB) and slope bias (SB) to identify potential systematic biases:

$$\text{MB} = (\overline{O} - \overline{P})^2$$

$$\text{SB} = (S_p - rS_o)^2$$

where $\overline{O}$ and $\overline{P}$ denote the predicted and observed means, S_p, and S_o the standard deviation of predicted and observed values, respectively, and r the Pearson correlation coefficient. The RMSPE to standard deviation ratio of observed values (RSR) was also calculated:

$$\text{RSR} = \frac{\text{RMSPE}}{S_o}$$

where S_o denotes the standard deviation of observations. Accordingly, RSR was used to evaluate the prediction performance of each model in relation to the variability of the different databases (Moriasi et al., 2007). Furthermore, the concordance correlation coefficient (CCC), which quantifies both accuracy and precision by comparing the degree of deviation between the best-fit line and the identity line ($y = x$), was calculated as follows (Lin, 1989):

$$CCC = r \bullet C_b$$

where r represents the Pearson correlation coefficient and C_b the bias correction factor as follows.

$$C_b = \left[\left(v + 1/v + u^2\right)/2\right]^{-1}$$

$$v = S_o \,/\, S_p$$

$$u = (\overline{P} - \overline{O})/(S_o S_p)^{1/2}$$

where, $\overline{O}$, $\overline{P}$, S_o and S_p were defined above, v denotes a measure of scale fit and u provides a measure of location shift. In general, low RMSPE and RSR values imply better model performance and prediction accuracy, where the closer the CCC of a model to 1, the better model performance. Since RSR is weighed by the variation across the observations, it is considered a reliable metric when comparing models developed with different numbers of observations. Different forage content cut-offs were evaluated (100, 95, 90, 85, 80, 75 and 70% of forage in the diet) for splitting the database into FD and MD subsets. The optimal cut-off value was chosen based on the best performances of their DMI equations to predict CH_4 production while keeping sufficient number of observations in the MD database.

3. Results

The inclusion criteria used to develop the refined database (summarized in Table 1) had minor effects on most variable means in comparison with the initial dataset (Supplementary Table S1). The refined database had slightly higher values for CH_4 production (19.7 *vs.* 19.5 g/d) and CH_4 yield (19.9 *vs.* 19.8 g/kg DMI) than the original database because data from all CH_4 mitigation treatments were removed (26% of the data). Outliers represented a minor proportion of the data (1.8%) with a similar representation for the low- and high-ends of CH_4 yield. The separation of the refined database into subsets according to animal age (Table 1), type of diet and climatic region (Table 2) also modulated the variables. For example, adult sheep compared to young sheep showed higher BW (52.1 *vs.* 34.1 kg), DMI (1.05 *vs.* 0.94 kg/d), CH_4 production (21.3 *vs.* 17.0 g/d), CH_4 yield (20.7 *vs.* 18.6 g/kg DMI) and Y_m (6.59 *vs* 5.86% GEI). The FD subset compared to the MD subset had a higher forage inclusion ratio (100 *vs.* 73.4% DMI), ash content (8.95 *vs.* 6.65% DM), CH_4 yield (20.3 *vs.* 18.0 g/kg DMI), and Y_m (6.44 *vs.* 5.71% GEI), and a lower total VFA concentration (87.0 vs. 79.0 mmol/L). Across climatic regions, the warm climate subset compared to the temperate climate subset showed slightly higher dietary NDF (53.6 vs. 48.3% DM), ADF (30.0 vs. 25.7% DM), acetate to propionate ratio (3.57 vs. 3.43) and CH_4 production (21.3 vs. 18.6 g/d).

3.1. Universal CH_4 production models

Universal CH_4 prediction equations with $P < 0.05$ are illustrated in Table 3 and 95% confidential interval of the regression coefficient can be estimated as $\pm$ 2 $\times$ SE. Equation 1 indicated a positive relationship between DMI and CH_4 production across the entire database (RMSPE = 25.4%, RSR = 0.69, CCC = 0.66) similar to that observed in the GEI equation (Eq. 2). The inclusion of DMI + BW (Eq. 3) resulted in RMSPE of 23.3%, RSR of 0.62 and CCC of 0.73, with additional improvement obtained by the DMI + OMD + BW equation (Eq. 4, RMSPE = 20.1%, RSR = 0.60, CCC = 0.77). Prediction models showed that, after excluding all CH_4 mitigating dietary treatments, the diet composition had a small impact on CH_4 production. As a result, only DMI and dietary ash content were selected for the Diet equation (Eq. 5), which hardly improved the prediction performance of the DMI equation. Alternative models including DMI + For, DMI + NDF, DMI + EE, DMI + CP were also evaluated but did not increase the prediction performance (data not shown). An increase in the performance was noted when dietary composition and BW were considered in the Animal equation (Eq. 6, RMSPE = 22.9%, RSR = 0.61, CCC = 0.74). On the contrary, the Animal_no_DMI equation (Eq. 7) had the poorest prediction performance

Table 2
Summary statistics for forage and mixed diets and for temperate and warm climatic conditions subsets.

	Forage diets (n = 1,797)				Mixed diets (n = 338)				Temperate climate (n = 1,222)				Warm climate (n = 913)			
	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD	Mean	Min	Max	SD
Dry matter intake (kg/d)	1.00	0.32	2.74	0.34	1.07	0.22	2.13	0.40	0.96	0.32	2.13	0.33	1.08	0.22	2.74	0.37
GE intake (MJ/d)	17.6	5.64	48.8	6.10	18.7	3.88	35.6	6.85	17.0	5.64	38.1	5.84	18.8	3.88	48.8	6.58
Body weight (kg)	46.6	18.0	97.0	12.6	39.7	15.0	112	21.6	45.4	19.3	112	13.3	46.0	15.0	97.0	15.3
Diet composition (% of DM)																
Crude protein	15.0	3.11	29.7	4.36	13.8	4.81	24.3	4.40	15.0	3.11	27.3	4.45	14.5	3.55	29.7	4.29
Ether extract	2.67	0.69	5.10	0.80	3.45	0.97	8.47	1.63	2.83	0.69	5.80	0.72	2.76	0.97	8.47	1.32
Ash	8.95	2.49	20.6	2.65	6.65	2.89	11.4	1.48	8.45	2.49	20.6	2.84	8.77	2.72	15.5	2.32
Neutral detergent fibre	51.0	15.2	78.4	9.21	52.1	26.1	80.5	11.9	49.3	15.2	77.0	9.80	53.6	26.1	80.5	8.98
Acid detergent fibre	27.4	8.17	43.8	5.09	28.1	12.9	47.4	7.19	25.7	8.17	39.2	4.76	30.0	12.9	47.4	5.41
GE (MJ/kg DM)	17.5	15.1	19.1	0.49	17.6	15.5	20.1	0.90	17.6	15.7	20.1	0.57	17.5	15.1	19.2	0.58
Forage (% of DM)	100	99.6	100	0.02	73.4	20.6	94.4	15.8	97.1	20.6	100	9.73	94.1	40.0	100	13.4
Rumen parameters																
Rumen pH	6.76	5.62	7.70	0.30	6.72	6.21	7.21	0.22	6.76	5.62	7.70	0.29	6.67	6.21	7.10	0.21
Ammonia-N (mmol/L)	9.88	1.18	54.5	7.32	20.5	1.15	63.6	17.9	10.5	1.15	54.5	8.39	15.9	1.60	63.6	15.81
Total VFA (mmol/L)	79.0	23.6	181	20.8	87.0	16.5	171	32.7	78.0	23.6	181	21.3	91.6	16.5	171	28.53
Acetate (%)	65.4	48.4	81.7	6.15	63.2	40.3	86.9	12.0	65.4	48.4	81.7	6.23	63.3	40.3	86.9	11.6
Propionate (%)	20.4	8.08	36.2	4.34	20.2	8.70	32.6	5.55	20.4	8.08	36.2	4.41	20.0	8.70	32.6	5.28
Butyrate (%)	10.1	0.49	24.8	3.16	11.9	2.59	25.4	5.94	10.2	0.49	24.8	3.22	11.3	2.59	25.4	5.83
Acetate to propionate ratio	3.43	1.43	9.75	1.14	3.58	1.23	9.99	1.83	3.43	1.43	9.75	1.15	3.57	1.23	9.99	1.76
OM digestibility (%)	65.7	44.8	93.5	9.68	65.6	35.1	90.8	13.9	69.1	44.8	93.5	10.9	64.0	35.1	90.8	10.0
Methane (CH_4) emissions																
CH_4 production (g/d)	19.9	3.57	57.1	6.89	19.1	3.69	44.8	9.14	18.6	4.62	44.8	6.16	21.3	3.57	57.1	8.34
CH_4 yield (g/kg DMI)	20.3	6.84	32.7	4.49	18.0	6.86	33.2	5.32	19.9	6.86	32.6	4.55	19.9	6.84	33.2	4.92
Y_m (% of GE intake)	6.44	2.11	10.8	1.44	5.71	2.21	10.5	1.71	6.30	2.18	10.8	1.45	6.36	2.11	10.6	1.59

GE = gross energy; VFA = volatile fatty acids; OM = organic matter; Y_m = CH_4 emission factor. Forage diet (≥95% forage); mixed diet (<95% forage); Temperate climates included studies from New Zealand, the United Kingdom, Norway, Switzerland, and Canada. Warm climate included studies from Australia, Brazil, France (French West Indies), Mexico, Argentina, Spain, Peru, and Egypt.

Table 3
Universal CH_4 production (g/d per sheep) prediction equations for various categories and model performance across the data subsets.

					Model performance				
Eq.	Category	Prediction equation	Subset	*n*	RMSPE	RSR	MB	SB	CCC
[1]	DMI	6.29 (0.533) + 12.6 (0.300) × DMI	All data	2,135	25.4	0.69	1.81	3.20	0.66
			Adult	1,374	23.8	0.70	11.3	3.65	0.66
			Young	761	29.2	0.75	5.67	0.14	0.61
			FD	1,797	23.4	0.68	4.08	3.38	0.68
			MD	338	34.9	0.73	1.21	4.20	0.60
			Temp.	1,222	24.1	0.73	0.08	0.03	0.64
			Warm	913	26.6	0.68	6.18	11.2	0.66
[2]	GEI	[0.358 (0.0299) + 0.0393 (0.000942) × GEI] / 0.05565	All data	2,135	25.7	0.70	2.15	3.31	0.65
			Adult	1,374	24.1	0.71	12.4	3.51	0.65
			Young	761	29.3	0.76	5.63	0.31	0.60
			FD	1,797	23.7	0.68	4.55	3.25	0.67
			MD	338	35.4	0.74	0.85	5.27	0.57
			Temp.	1,222	24.3	0.73	0.09	0.01	0.63
			Warm	913	27.0	0.69	7.40	11.2	0.65
[3]	DMI+BW	2.47 (0.569) + 10.2 (0.346) × DMI + 0.140 (0.0115) × BW	All data	1,810	23.3	0.62	0.31	2.87	0.73
			Adult	1,165	23.2	0.66	0.99	2.83	0.69
			Young	645	23.0	0.68	0.23	1.16	0.67
			FD	1,566	23.3	0.66	0.53	1.83	0.70
			MD	244	23.4	0.49	0.45	12.2	0.84
			Temp.	905	21.5	0.70	5.73	1.27	0.71
			Warm	905	24.4	0.62	7.39	7.83	0.73
[4]	DMI+OMD+BW	-0.669 (1.40) + 9.19 (0.453) × DMI + 0.0495 (0.0170) × OMD + 0.169 (0.0159) × BW	All data	1,020	20.1	0.60	0.26	0.84	0.77
			Adult	716	19.0	0.68	1.72	0.01	0.70
			Young	304	23.6	0.70	2.90	0.76	0.66
			FD	824	19.9	0.67	0.49	0.00	0.71
			MD	196	20.9	0.45	0.16	18.5	0.87
			Temp.	333	19.1	0.68	10.2	7.22	0.76
			Warm	687	20.5	0.59	3.92	4.41	0.77
[5]	Diet	4.10 (0.660) + 12.57 (0.296) × DMI + 0.261 (0.0458) × ASH	All data	2,135	25.3	0.68	1.64	3.08	0.67
			Adult	1,374	23.5	0.69	12.2	3.33	0.67
			Young	761	29.3	0.75	7.54	0.29	0.61
			FD	1,797	23.2	0.67	3.05	2.83	0.69
			MD	338	34.8	0.73	0.14	4.46	0.60
			Temp.	1,222	24.3	0.73	0.08	0.04	0.64
			Warm	913	26.1	0.67	5.71	11.1	0.67
[6]	Animal	0.432 (0.676) + 10.2 (0.343) × DMI + 0.244 (0.0446) × ASH + 0.138 (0.0114) × BW	All data	1,810	22.9	0.61	0.24	3.34	0.74
			Adult	1,165	22.8	0.65	1.51	2.83	0.71
			Young	645	22.7	0.68	1.66	0.75	0.69
			FD	1,566	22.8	0.64	0.24	2.56	0.72
			MD	244	23.6	0.49	0.22	11.8	0.84
			Temp.	905	21.0	0.69	6.64	0.52	0.72
			Warm	905	24.0	0.61	7.33	7.35	0.74
[7]	Animal_no_DMI	-16.6 (6.06) - 0.0916 (0.0304) × ADF + 0.290 (0.0709) × ASH + 1.22 (0.323) × GE + 0.303 (0.0124) × BW	All data	1,810	31.3	0.84	1.41	0.71	0.50
			Adult	1,165	31.7	0.90	2.33	1.67	0.40
			Young	645	29.1	0.86	0.12	1.96	0.47
			FD	1,566	31.2	0.88	1.40	0.55	0.42
			MD	244	31.9	0.66	1.51	2.40	0.75
			Temp.	905	29.9	0.98	8.43	11.4	0.45
			Warm	905	32.0	0.82	19.0	2.14	0.54
[8]	Animal_VFA	10.18 (1.50) + 12.5 (0.780) × DMI - 0.438 (0.0376) × Pro + 0.116 (0.0275) × BW	All data	584	20.0	0.64	0.69	0.54	0.77
			Adult	286	19.7	0.60	8.70	2.79	0.82
			Young	298	20.3	0.76	2.17	0.10	0.65
			FD	468	18.9	0.66	0.70	0.38	0.75
			MD	116	23.9	0.60	0.71	1.0	0.80
			Temp.	461	18.4	0.66	0.57	0.03	0.76
			Warm	123	23.7	0.66	1.14	3.29	0.76
[9]	Global	-29.6 (2.71) + 12.5 (0.766) × DMI + 0.113 (0.0160) × NDF + 0.112 (0.0380) × CP + 0.301 (0.0367) × Ace + 0.421 (0.0511) × But + 0.120 (0.0273) × BW	All data	584	20.3	0.65	0.00	1.04	0.76
			Adult	286	19.3	0.59	2.02	0.80	0.81
			Young	298	21.4	0.81	1.90	4.19	0.62
			FD	468	20.4	0.71	0.11	3.24	0.71
			MD	116	20.0	0.50	1.51	2.31	0.87
			Temp.	461	20.0	0.71	0.00	1.67	0.71
			Warm	123	21.0	0.58	0.00	0.37	0.81
[10]	IPCC_2006	0.065 [or 0.045] x GEI / 0.05565 for adult [or young sheep]	All data	2,135	27.1	0.73	4.23	15.9	0.75
[11]	IPCC_2019_fix	0.067 x GEI / 0.05565	All data	2,135	28.1	0.76	8.97	14.0	0.73
[12]	IPCC_2019_var	0.070 [or 0.067 or 0.065] x GEI / 0.05565 when DMI <0.6 [or 0.6-0.8 or >0.8] kg/d	All data	2,135	26.8	0.73	5.10	10.0	0.73

In grey is indicated the database used for model development and evaluation. Equations are presented with regression coefficient standard errors in parenthesis. RMSPE, Root mean square prediction error, expressed as a percentage of observed CH_4 emission means; RSR, RMSPE-observations standard deviation ratio; MB, mean bias as a percentage of MSPE; SB, slope bias as a percentage of MSPE; CCC, Concordance Correlation Coefficient; FD, forage diet (≥95% forage); MD, mixed diet (<95% forage); Temp, temperate climate; Warm, Warm climate; DMI, dry matter intake (kg/d); GEI, gross energy intake (MJ/d); BW, body weight (kg); OMD, organic matter digestibility (%); IPCC, Intergovernmental Panel on Climate Change; ash, dietary ash (% of DM); NDF, dietary neutral detergent fibre (% of DM); ADF, dietary acid detergent fibre (% of DM); GE, dietary gross energy (MJ/kg DM); CP, dietary crude protein (% DM); Ace, acetate (%); Pro, propionate (%); But, butyrate (%).

due to the absence of the DMI as a key variable. The Animal_VFA equation (Eq. 8) showed that rumen propionate proportion was negatively correlated with CH_4 production, and when used in conjunction with DMI and BW, resulted in the lowest RMSPE (20.0%) and highest CCC values (0.77), but did not outperform the DMI + BW, DMI + OMD + BW and Animal models in terms of RSR. The incorporation of additional rumen fermentation data including rumen pH and concentrations of ammonia and total VFA decreased the number of observations and did not improve the Animal_VFA equations (data not shown); therefore, they were not further considered. The more complex Global equation (Eq. 9) selected DMI, NDF, CP, acetate, butyrate and BW as the key variables, all of which positively correlated with CH_4 production;

however, this increase in complexity did not increase prediction performance (RMSPE = 20.2%, RSR = 0.65, CCC = 0.76) compared with previous models.

The IPCC, 2006 equation (Eq. 10) showed lower prediction performance (RMSPE = 27.1%, RSR = 0.73, CCC = 0.75) than our Y_m GEI equation (Eq. 2) except for CCC. The prediction performance was slightly better for the IPCC_2019_var (Eq. 12) than for the IPCC_2019_fix (Eq. 11) equations (RMSPE = 26.8% vs. 28.1%, RSR = 0.73 vs. 0.76) but weaker than the Y_m GEI equation (Eq. 2). In particular, the IPCC_2019 equations showed a higher slope bias than those developed in the present study which was consistently associated with under-prediction at the low end and over-prediction at the high end of CH_4 production (Fig. 1). The developed universal equations using the refined database were also evaluated for the age-, diet-, and climatic region-specific databases which differed in size (Table 3). The RSR showed that the equations that did not include BW, such as the DMI (Eq. 1), GEI (Eq. 2) or Diet (Eq. 5) consistently had lower prediction performances for young than for adult sheep and for MD than for FD databases.

3.2. Age-specific CH_4 production models

The development of adult sheep-specific equations (Table 4) based on DMI (Eq. 13), GEI (Eq. 14) and Diet (Eq. 16, including DMI and NDF) resulted in higher prediction performances (average RSR = 0.66) than reported for their equivalent universal equations applied to adult sheep (Eqs. 1, 2 and 5, average RSR = 0.70) or for IPCC equations (Eqs. 21, 22, 23, average RSR = 0.70). The Animal equation (Eq. 17) only selected DMI and BW as the predictor variables resulting in similar prediction performance (RSR = 0.66) to previous equations. Similarly, the DMI + OMD + BW equation (Eq. 15) did not outperform the equivalent universal equation (Eq. 4, Fig. 2). On the contrary, for adult sheep the Animal_VFA (Eq. 19, including DMI and propionate) and Global equations (Eq. 20, including DMI, ADF, and propionate) showed a prediction performance (RMSPE = 18.6 and 17.9%, RSR = 0.57 and 0.55, respectively) substantially improved compared to those reported for their equivalent universal equations applied to adult sheep (Eqs. 8 and 9, RMSPE = 19.7 and 19.3%, RSR = 0.60 and 0.59, respectively). As observed with the universal models, the Animal_no_DMI equation (Eq. 18) had the weakest prediction performance. The IPCC equations (Eq. 21, 22, and 23) had similar performances for adult sheep (average RMSPE = 23.6%, RSR = 0.70, CCC = 0.77) as observed for the DMI equation but with a substantially higher slope bias. The evaluation of the adult sheep-specific equations across smaller databases allowed exploring their potential and drawbacks when applied to different diets or climates (Supplementary Table S2). The proposed equations based on DMI (Eq. 13), GEI (Eq. 14), Diet (Eq. 16) and Animal_VFA (Eq. 19)

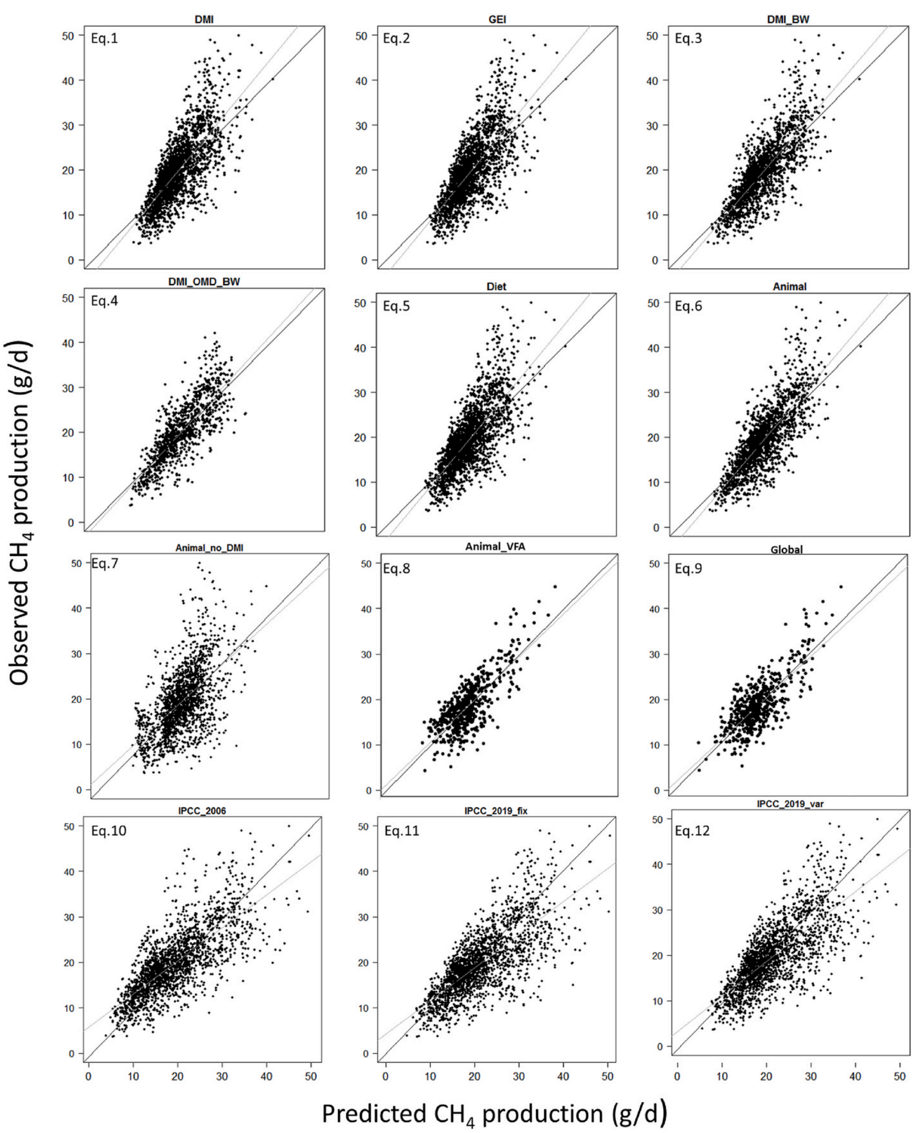

Fig. 1. Observed *vs.* predicted plots for universal CH_4 production (g/d per animal) prediction equations at different complexity levels of DMI (Eq. 1), GEI (Eq. 2), DMI + BW (Eq. 3), DMI + OMD + BW (Eq. 4), Diet (Eq. 5 included DMI and diet composition variables), Animal (Eq. 6 included DMI, diet composition, and BW), Animal_no_DMI (Eq. 7 included diet composition and BW), Animal_VFA (Eq. 8 included DMI, rumen VFA, and BW), Global (Eq. 9 included all available variables), IPCC, 2006 (Eq. 10), IPCC, 2019 fixed emission factors (Eq. 11) and IPCC, 2019 variable emission factor (Eq. 12) according to DMI. The grey and black solid lines represent the fitted regression line for the relationship between the predicted and observed values and the identity line ($y = x$), respectively.

Table 4
Age-specific CH_4 production (g/d per sheep) prediction equations for adult (>1 yr old) and young sheep (<1 yr old).

Eq.	Category	Prediction equation	*n*	Subset	Model performance RMSPE	RSR	MB	SB	CCC
[13]	DMI	7.82 (0.699) + 12.7 (0.341) × DMI	1,374	Adult	22.4	0.66	0.00	3.47	0.69
[14]	GEI	[0.443 (0.0392) + 0.0397 (0.00109) × GEI] / 0.05565	1,374	Adult	22.6	0.67	0.06	3.32	0.68
[15]	DMI+OMD+BW	-4.32 (2.04) + 9.57 (0.532) × DMI + 0.126 (0.0240) × OMD + 0.145 (0.0190) × BW	716	Adult	19.4	0.69	0.08	0.02	0.68
[16]	Diet	13.0 (1.09) + 12.6 (0.337) × DMI - 0.103 (0.0160) × NDF	1,374	Adult	22.2	0.66	0.16	3.06	0.70
[17]	Animal; DMI+BW	4.62 (0.867) + 10.5 (0.412) × DMI + 0.108 (0.0129) × BW	1,165	Adult	23.0	0.66	0.36	5.00	0.69
[18]	Animal_no_DMI	14.6 (1.73) - 0.248 (0.0399) × ADF + 0.252 (0.0155) × BW	1,165	Adult	31.8	0.91	0.97	0.19	0.33
[19]	Animal_VFA	14.7 (1.63) + 15.4 (1.01) × DMI - 0.487 (0.0580) × Pro	286	Adult	18.6	0.57	0.01	1.36	0.82
[20]	Global	8.15 (2.66) + 15.4 (0.985) × DMI + 0.235 (0.0782) × ADF - 0.454 (0.0577) × Pro	286	Adult	17.9	0.55	0.04	2.51	0.84
[21]	IPCC_2006	0.065 x GEI / 0.05565 for adult sheep	1,374	Adult	23.4	0.69	0.29	13.6	0.77
[22]	IPCC_2019_fix	0.067 x GEI / 0.05565	1,374	Adult	24.1	0.71	3.30	16.1	0.76
[23]	IPCC_2019_var	0.070 (or 0.067 or 0.065) x GEI / 0.05565 when DMI < 0.6 or 0.6-0.8 or >0.8 kg/d	1,374	Adult	23.2	0.68	0.73	11.6	0.77
[24]	DMI	5.63 (0.701) + 11.0 (0.564) × DMI	761	Young	29.5	0.76	3.89	2.02	0.57
[25]	GEI	[0.317 (0.0386) + 0.0344 (0.00175) × GEI] / 0.05565	761	Young	29.7	0.77	4.23	2.43	0.56
[26]	DMI+BW	2.12 (0.865) + 9.49 (0.615) × DMI + 0.143 (0.0270) × BW	645	Young	23.9	0.71	3.50	2.16	0.64
[27]	DMI+OMD+BW	2.94 (1.94) + 8.20 (0.925) × DMI - 0.0311 (0.0225) × OMD + 0.215 (0.0387) × BW	304	Young	25.0	0.74	2.91	0.36	0.65
[28]	Diet	0.982 (1.287) + 11.5 (0.571) × DMI + 0.158 (0.0360) × ADF	761	Young	29.7	0.77	3.79	0.85	0.57
[29]	Animal	-1.45 (1.88) + 9.64 (0.622) × DMI + 0.115 (0.0185) × NDF +0.280 (0.0793) × ASH - 0.0510 (0.0160) × For + 0.123 (0.0280) × BW	645	Young	26.5	0.79	5.88	0.01	0.57
[30]	Animal_no_DMI	3.15 (2.26) + 0.0847 (0.0201) × NDF + 0.186 (0.0420) × CP - 0.0906 (0.0184) × For + 0.370 (0.0276) × BW	645	Young	33.2	0.99	6.44	7.95	0.36
[31]	Animal_VFA	-32.6 (3.76) + 10.5 (1.09) × DMI + 0.438 (0.0478) × Ace + 0.552 (0.0771) × But + 0.142 (0.0408) × BW	298	Young	23.2	0.88	0.02	1.98	0.44
[32]	Global	-26.1 (3.33) + 11.5 (0.989) DMI + 0.145 (0.0175) × NDF +0.230 (0.0466) × Ace + 0.549 (0.0702) × But + 0.127 (0.0347) × BW	298	Young	20.5	0.77	1.75	0.77	0.60
[33]	IPCC_2006	0.045) x GEI / 0.05565 for young sheep	761	Young	35.3	0.91	35.7	0.18	0.54
[34]	IPCC_2019_fix	0.067 x GEI / 0.05565	761	Young	36.6	0.94	22.9	17.3	0.62
[35]	IPCC_2019_var	0.070 (or 0.067 or 0.065) x GEI / 0.05565 when DMI < 0.6 (or 0.6-0.8 or >0.8) kg/d	761	Young	34.7	0.89	19.4	13.7	0.63

Equations are presented with regression coefficient standard errors in parenthesis ; RMSPE, Root mean square prediction error, expressed as a percentage of observed CH_4 emission means; RSR, RMSPE-observations standard deviation ratio; MB, mean bias as a percentage of MSPE; SB, slope bias as a percentage of MSPE; CCC, Concordance Correlation Coefficient; DMI, dry matter intake (kg/d); GEI, gross energy intake (MJ/d); BW, body weight (kg); OMD, organic matter digestibility (%); VFA, volatile fatty acids, IPCC, Intergovernmental Panel on Climate Change; ASH, ash content (% DM); NDF, dietary neutral detergent fibre (% DM); ADF, dietary acid detergent fibre (% DM); For, forage %,; Ace, acetate (%); Pro, propionate (%); But, butyrate (%).

showed potential to be used for adult sheep fed FD and MD as they had similar RSR values, but these equations had slightly lower prediction performances for temperate than for warm climate-regions.

The development of young sheep-specific equations based on DMI (Table 4, Eq. 24) resulted in similar prediction performances to the universal equations applied to young sheep (RMSPE = 29.5 vs. 29.2%, RSR = 0.76 vs. 0.75, CCC = 0.57 vs. 0.61). The inclusion of DMI + BW (Eq. 26) in the equations led to high prediction performance (RMSPE = 23.9%, RSR = 0.71) but did not outperform the equivalent universal equation applied to young sheep (Eq. 3). The inclusion of additional data such as OMD (Eq. 26), diet composition (Eqs. 27 and 28) or rumen VFA (Eqs. 30 and 31) did not further improve the DMI + BW prediction performance, but decreased the number of observations, suggesting that DMI and BW are the key variables to predict CH_4 production in young sheep. The Global equation (Eq.32, Fig. 2) which included DMI, NDF, acetate, butyrate and BW led to the lowest RMSPE value and slightly outperformed its equivalent universal equation (Eq. 9) which also included CP as a predictor variable (RSR = 0.77 vs 0.81). All young sheep-specific equations (including DMI and GEI equations) led to higher prediction performance than the IPCC equations (Eqs. 33, 34, and 35) suggesting that IPCC equations are inaccurate for young sheep. The IPCC_2006 equation (Eq. 33) showed a negligible slope bias when applied to < 1-year-old sheep, whereas the IPCC_2019 equations (Eq. 34 and 35) showed the highest slope bias across all equations, indicating an under-estimation of the low-end CH_4 production (Supplementary Fig. S2). The prediction performances of the young sheep-specific equations were moderately affected by the type of diet and climatic region (Supplementary Table S3), being slightly better for FD than for MD or for temperate than for warm climate.

3.3. Diet-specific CH_4 production models

Different cut-off values for the dietary forage proportion were evaluated to develop diet-specific equations (Supplementary Table S4). Decreasing the forage proportion cut-off value from 100 to 70% resulted in very similar RSR (from 0.67 to 0.68) and CCC values (from 0.69 to 0.67) for the FD database but led to a substantial decrease in the CCC values (from 0.51 to 0.40) and the number of observations (from 342 to 184) in the MD database. As a result, a cut-off value of 95% of dietary forage content was chosen to keep a sufficient number of observations for the MD database without compromising the prediction performance. This separation also reflects the main sheep production systems: i) the extensive systems based entirely on grazing (FD) and ii) the semi-intensive systems in which sheep are supplemented with varying levels of concentrate (equivalent to MD).

The development of an FD-specific equation (Table 5) based on DMI led to minor improvements in prediction performance in relation to the universal equations applied to FD (Eq. 36 vs 1, RMSPE = 23.2 vs 23.4%, RSR = 0.67 vs 0.68, CCC = 0.69 vs 0.68, Fig. 2). Similar improvements were noted for the GEI equation (Eq. 37, RSR = 0.67). The increase in model complexity in DMI + BW (Eq. 38), Diet (Eq. 39) and Animal (Eq. 41) equations led to similar prediction performances (average RMSPE = 23.3%, RSR = 0.67, CCC = 0.69) to the DMI equation indicating a high CH_4 prediction capacity for the DMI but low for the diet composition and BW in animals fed FD. The DMI + OMD + BW, Animal_VFA and Global equations (Eqs. 39, 43 and 44) had similar prediction performance to the simpler equations (Eq. 36) and underperformed their equivalent universal equations applied to FD. In comparison to FD-specific equations (Eqs. 36 and 37), the IPCC equations (Eqs. 45, 46 and 47) showed weaker CH_4 prediction performances when applied to animals fed FD (average RMSPE = 25.3%, RSR = 0.73, CCC = 0.75), as well as a higher slope bias, as described before. Most of the FD-specific equations showed

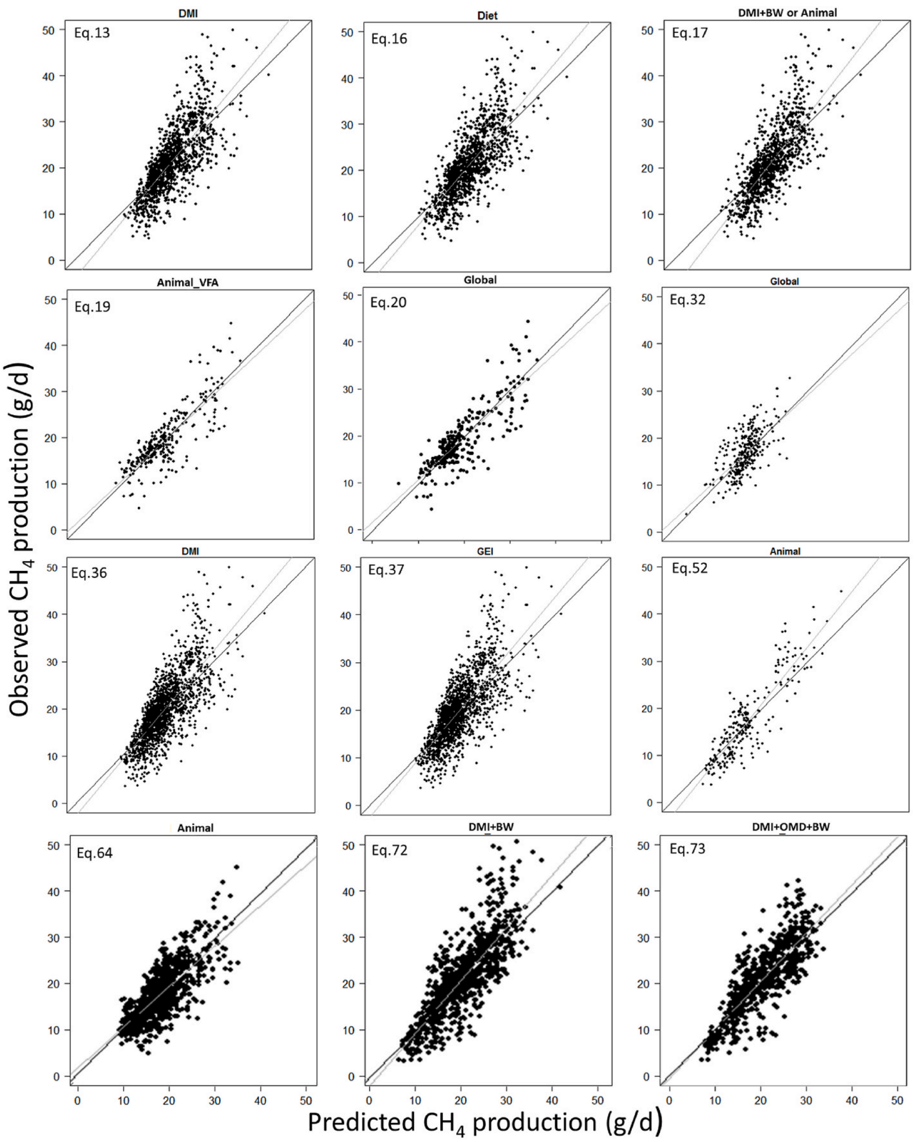

Fig. 2. Observed *vs.* predicted plots for the most promising CH_4 production (g/d per animal) prediction equations at different complexity levels for adult sheep (Eqs. 13, 16, 17, 19 and 20), young sheep (Eq. 32), forage diets (Eq. 36 and 37), mixed diets (Eq. 52), temperate- (Eq. 64) and warm climatic-regions (Eqs. 72 and 73). Diet equations included DMI and diet composition variables, Animal equations included DMI, diet composition, and BW, Animal_VFA equations included DMI, rumen VFA, and BW, Global equations included all available variables. The grey and black solid lines represent the fitted regression line for the relationship between the predicted and observed values and the identity line ($y = x$), respectively.

similar CH_4 prediction performances for both climatic regions but slightly higher for adult sheep than young sheep fed FD (Supplementary Table S5).

The MD subset had a forage proportion that varied from 20.6 to 94.4% of DMI (average 73.4%). This MD database only represented 16% of the data in the refined database, and two-thirds of it corresponded to young sheep; therefore, the developed MD-specific equations should be carefully interpreted given the limited number of observations (Table 5). The universal IPCC_2019_var equation (Eq. 12) did not show high CH_4 prediction performance when applied to animals fed MD (average RMSPE = 38.2%, RSR = 0.80, CCC = 0.65). The development of MD-specific equations did not substantially improve the prediction capacity in comparison to the universal equations applied to animals fed MD. The Diet equation only selected DMI as the key CH_4 variable (Eq. 48), and had a limited prediction performance (RMSPE = 36.8%, RSR = 0.77, CCC = 0.51). The models that also included BW as a variable such as the DMI + BW (Eq. 50), DMI + OMD + BW (Eq. 51), Animal (Eq. 52; Fig. 2), and Animal_no_DMI (Eq. 53) equations had higher CH_4 prediction performance (average RMSPE = 24.0%, RSR = 0.50, CCC = 0.84), and the Animal equation (including DMI, GE and BW) was able to outperform its equivalent universal equation (Eqs. 52 vs 6; RMSPE = 23.1 vs 23.6, RSR = 0.48 vs 0.49). The inclusion of rumen VFA (Eqs. 54 and 55) resulted in lower prediction performances (RSR = 0.64 and 0.79) than observed with their equivalent universal equations (Eqs. 8 and 9, RSR = 0.60 and 0.50, respectively). The MD-specific equations had superior prediction performance for adult sheep than for young sheep, as was also the case for the IPCC equations (Suppl. Table S6).

3.4. Climatic region-specific CH_4 production models

The climate region-specific equations had a minor impact on the prediction performance (Table 6). Dry matter intake was again the key predictor variable followed by BW. For temperate climatic regions, the models including DMI (Eq 59), GEI (Eq. 60), DMI + BW (Eq. 61), DMI + BW + OMD (Eq. 62) and the Diet equation (Eq. 63) had prediction performances similar to that observed for the universal equations applied to this database (Table 3). The Animal equation, including DMI, EE, GE and BW as the predictor variables, represented the model with the highest prediction performance for temperate regions (Eq. 64, RMSPE = 20.7, RSR = 0.68, Fig. 2), and it outperformed its universal counterpart equation (Eq. 6). The Animal_VFA equation (Eq. 66) also led to high prediction performance but did not outperform the equivalent universal equation (Eq. 8).

The specific equations for warm climatic-regions did not improve the

Table 5
Diet-specific CH_4 production (g/d per sheep) prediction equations for sheep fed forage (FD) or mixed diets (MD).

Eq.	Category	Prediction equation	*n*	Subset	Model performance				
					RMSPE	RSR	MB	SB	CCC
[36]	DMI	6.41 (0.505) + 12.8 (0.303) × DMI	1,797	FD	23.2	0.67	1.62	2.57	0.69
[37]	GEI	[0.367 (0.0281) + 0.0401 (0.000956) × GEI] / 0.05565	1,797	FD	23.3	0.67	1.55	2.34	0.68
[38]	DMI+BW	2.94 (0.638) + 10.3 (0.368) × DMI + 0.133 (0.0127) × BW	1,566	FD	23.4	0.66	0.06	2.00	0.70
[39]	DMI+OMD+BW	-2.47 (1.87) + 9.19 (0.495) × DMI + 0.0801 (0.0216) × OMD + 0.167 (0.0193) × BW	824	FD	20.5	0.69	0.20	0.01	0.69
[40]	Diet	-31.4 (6.84) + 12.8 (0.300) × DMI + 0.590 (0.0846) × ASH - 0.148 (0.0416) × CP + 1.97 (0.376) × GE	1,797	FD	23.4	0.67	2.73	1.05	0.69
[41]	Animal	-1.69 (0.949) + 10.2 (0.363) × DMI + 0.172 (0.0480) × ASH + 1.09 (0.233) × EE + 0.135 (0.0127) × BW	1,566	FD	23.3	0.65	0.20	1.00	0.71
[42]	Animal_no_DMI	3.99 (1.46) - 0.139 (0.0296) × ADF + 1.81 (0.280) × EE + 0.306 (0.0136) × BW	1,566	FD	31.8	0.89	0.48	2.42	0.42
[43]	Animal_VFA	12.0 (1.74) + 12.9 (0.838) × DMI - 0.543 (0.0422) × Pro + 0.122 (0.0335) × BW	468	FD	20.3	0.71	0.08	4.28	0.71
[44]	Global	6.51 (2.08) + 13.4 (0.827) × DMI + 0.0816 (0.0169) × NDF - 0.465 (0.0446) × Pro + 0.114 (0.0333) × BW	468	FD	20.7	0.72	0.00	5.63	0.70
[45]	IPCC_2006	0.065 (or 0.045) x GEI / 0.05565 for adult (or young) sheep	1,797	FD	26.0	0.75	3.66	23.0	0.75
[46]	IPCC_2019_fix	0.067 x GEI / 0.05565	1,797	FD	25.5	0.74	6.75	16.7	0.75
[47]	IPCC_2019_var	0.070 (or 0.067 or 0.065) x GEI / 0.05565 when DMI < 0.6 or 0.6-0.8 or >0.8, respectively.	1,797	FD	24.4	0.70	3.16	12.2	0.76
[48]	DMI; Diet	7.73 (1.59) + 10.3 (1.11) × DMI	338	MD	36.8	0.77	0.13	9.56	0.51
[49]	GEI	[0.439 (0.0903) + 0.0316 (0.00354) × GEI] / 0.05565	338	MD	37.6	0.78	0.46	10.8	0.47
[50]	DMI+BW	2.20 (1.32) + 8.06 (1.11) × DMI + 0.175 (0.0293) × BW	244	MD	24.4	0.51	1.63	10.9	0.83
[51]	DMI+OMD+BW	4.72 (2.05) + 11.8 (1.36) × DMI - 0.0440 (0.0257) × OMD + 0.116 (0.0341) × BW	196	MD	22.9	0.49	0.61	11.7	0.84
[52]	Animal	26.0 (8.91) + 7.78 (1.10) × DMI - 1.35 (0.493) × GE + 0.190 (0.0278) × BW	244	MD	23.1	0.48	1.25	10.7	0.85
[53]	Animal_no_DMI	34.2 (9.83) -1.69 (0.545) × GE + 0.303 (0.0252) × BW	244	MD	25.6	0.53	4.21	2.14	0.82
[54]	Animal_VFA	4.40 (3.05) + 11.8 (1.86) × DMI - 0.118 (0.0759) × Pro + 0.106 (0.0521) × BW	116	MD	25.3	0.64	4.83	9.37	0.71
[55]	Global	-8.01 (1.46) + 5.37 (1.68) × DMI + 0.136 (0.0209) × NDF - 0.454 (0.144) × EE + 0.169 (0.0503) × But + 0.344 (0.0326) × BW	116	MD	24.3	0.79	2.37	2.31	0.60
[56]	IPCC_2006	0.065 (or 0.045) x GEI / 0.05565 for adult (or young) sheep	338	MD	32.8	0.69	7.38	0.00	0.71
[57]	IPCC_2019_fix	0.067 x GEI / 0.05565	338	MD	39.7	0.83	21.2	5.68	0.65
[58]	IPCC_2019_var	0.070 (or 0.067 or 0.065) x GEI / 0.05565 when DMI < 0.6 (or 0.6-0.8 or >0.8) kg/d	338	MD	38.2	0.80	16.9	3.49	0.65

Equations are presented with regression coefficient standard errors in parenthesis. RMSPE, Root mean square prediction error, expressed as a percentage of observed CH_4 emission means; RSR, RMSPE-observations standard deviation ratio; MB, mean bias as a percentage of MSPE; SB, slope bias as a percentage of MSPE; CCC, Concordance Correlation Coefficient; FD, forage diet (≥95% forage); MD, mixed diet (<95% forage); DMI, dry matter intake (kg/d); GEI, gross energy intake (MJ/d); BW, body weight (kg); OMD, organic matter digestibility (%); IPCC, Intergovernmental Panel on Climate Change; ASH, dietary ash (% of DM); NDF, dietary neutral detergent fibre (% of DM); EE, dietary ether extract (% of DM); GE, dietary gross energy (MJ/kg DM); CP, dietary crude protein (% DM); Pro, propionate (%); But, Butyrate (%).

Table 6
Climate region-specific CH_4 production (g/d per sheep) prediction equations from temperate of warm climates.

Eq.	Category	Prediction equation	n	Subset	Model performance				
					RMSPE	RSR	MB	SB	CCC
[59]	DMI	6.32 (0.617) + 12.7 (0.365) × DMI	1,222	Temp.	24.5	0.74	0.02	0.43	0.64
[60]	GEI	[0.355 (0.0342) + 0.0397 (0.00114) × GEI] / 0.05565	1,222	Temp.	24.7	0.75	0.01	0.45	0.63
[61]	DMI+BW; Global	4.05 (0.700) + 10.8 (0.421) × DMI + 0.0904 (0.0141) × BW	905	Temp.	21.4	0.70	4.87	0.74	0.70
[62]	DMI+OMD+BW	-0.564 (2.00) + 9.12 (0.612) × DMI - 0.0674 (0.0216) × OMD + 0.1381 (0.0222) × BW	333	Temp.	20.7	0.74	13.2	9.40	0.73
[63]	Diet	3.37 (0.614) + 12.8 (0.362) × DMI + 1.03 (0.219) × EE	1,222	Temp.	24.7	0.74	0.00	1.14	0.64
[64]	Animal	6.82 (2.53) + 10.98 (0.414) × DMI + 1.36 (0.215) × EE - 0.072 (0.0254) × For + 0.0866 (0.0144) × BW	905	Temp.	20.7	0.68	1.39	1.57	0.73
[65]	Animal_no_DMI	-14.8 (5.92) - 0.148 (0.0386) × ADF + 1.18 (0.296) × EE + 1.18 (0.363) × GE + 0.263 (0.0167) × BW	905	Temp.	29.6	0.97	0.21	13.5	0.42
[66]	Animal_VFA	-35.94 (3.00) + 13.4 (0.844) × DMI + 0.479 (0.038) × Ace + 0.439 (0.056) × But + 0.133 (0.029) × BW	461	Temp.	19.6	0.70	0.11	3.10	0.71
[67]	IPCC_2006	0.065 (or 0.045) x GEI / 0.05565 for adult (or young sheep)	1,222	Temp.	29.0	0.88	6.63	20.2	0.65
[68]	IPCC_2019_fix	(0.067 x GEI) / 0.05565	1,222	Temp.	30.0	0.91	11.1	24.9	0.66
[69]	IPCC_2019_var	0.070 (or 0.067 or 0.065) x GEI / 0.05565 when DMI < 0.6 (or 0.6-0.8 or >0.8) kg/d	1,222	Temp.	28.4	0.86	7.52	20.6	0.67
[70]	DMI; Animal_VFA; Global	6.38 (0.918) + 12.3 (0.508) x DMI	913	Warm	27.4	0.70	7.93	11.74	0.63
[71]	GEI	[0.369 (0.0518) + 0.0384 (0.00161) × GEI] / 0.05565	913	Warm	27.6	0.71	8.35	12.01	0.62
[72]	DMI+BW	0.884 (0.874) + 9.29 (0.564) x DMI + 0.203 (0.0184) x BW	905	Warm	23.9	0.61	4.31	2.58	0.76
[73]	DMI+OMD+BW	0.688 (1.923) + 9.718 (0.652) x DMI + 0.0140 (0.0264) x ODM + 0.179 (0.0207) x BW	687	Warm	20.3	0.58	2.21	0.60	0.79
[74]	Diet	7.70 (2.70) + 10.8 (0.507) x DMI - 0.114 (0.0311) x NDF + 1.06 (0.127) x ASH -0.640 (0.216) x EE	913	Warm	28.7	0.73	0.75	0.14	0.63
[75]	Animal	1.256 (2.28) + 8.32 (0.559) x DMI - 0.0916 (0.028) x NDF + 0.861 (0.122) x ASH + 0.179 (0.018) x BW	905	Warm	25.2	0.64	0.05	0.10	0.74
[76]	Animal_no_DMI	8.67 (2.57) - 0.195 (0.0312) x NDF + 0.969 (0.138) x ASH + 0.312 (0.0182) x BW	905	Warm	31.0	0.79	0.07	2.30	0.60
[77]	IPCC_2006	0.065 (or 0.045) x GEI / 0.05565 for adult (or young sheep)	913	Warm	24.9	0.64	1.82	12.13	0.80
[78]	IPCC_2019_fix	(0.067 x GEI) / 0.05565	913	Warm	25.8	0.66	6.43	6.13	0.78
[79]	IPCC_2019_var	0.070 (or 0.067 or 0.065) x GEI / 0.05565 when DMI < 0.6 (or 0.6-0.8 or >0.8) kg/d	913	Warm	25.0	0.64	2.61	3.35	0.78

Equations are presented with regression coefficient standard errors in parenthesis. RMSPE, Root mean square prediction error, expressed as a percentage of observed CH_4 emission means; RSR, RMSPE-observations standard deviation ratio; MB, mean bias as a percentage of MSPE; SB, slope bias as a percentage of MSPE; CCC, Concordance Correlation Coefficient; Temp, temperate climate; Warm, Warm climate; DMI, dry matter intake (kg/d); GEI, gross energy intake (MJ/d); BW, body weight (kg); OMD, organic matter digestibility (%); IPCC, Intergovernmental Panel on Climate Change; ASH, dietary ash (% of DM); NDF, dietary neutral detergent fibre (% DM); EE, dietary ether extract (% of DM); GE, dietary gross energy (MJ/kg DM); For, forage (% DM); Ace, propionate (%); But, butyrate (%).

prediction performance when using DMI (Eq. 70) or GEI alone (Eq 71), but slight improvements were observed for DMI + BW (Eq. 72) and DMI + OMD + BW (Eq. 73, Fig. 2) which led to higher prediction performances than observed for their equivalent universal equations applied to warm-climates. Diet composition data had a negligible prediction ability in warm climate regions as noted by lower prediction performances in the Diet (Eq. 74), Animal (Eq. 75) and Global equations (Eq. 70).

3.5. Universal CH_4 yield models

The universal models developed to predict CH_4 yield (g/kg DMI) showed substantially weaker prediction performance than those predicting CH_4 production (Table 7 and Fig. 3). Moreover, these models should be carefully interpreted given the fact that the variable DMI was already included in the CH_4 yield being expressed per unit of DMI. Dry matter intake was negatively correlated with CH_4 yield (Eq. 80) but had a very low prediction performance (RMSPE = 23.5%, RSR = 1.00, CCC = 0.17). The Diet equation (Eq. 83) did not provide any further improvement in prediction performance. The DMI + BW equation (Eq. 81) demonstrated that BW positively correlates with CH_4 yield, but the prediction performance remained low (RMSPE = 22.0%, RSR = 0.95, CCC = 0.29) and similar to that observed for the Animal equation (Eq. 84). The DMI + OMD + BW equation indicated that OMD also positively correlates with CH_4 yield and led to a significant increase in prediction performance (RMSPE = 19.9%, RSR = 0.87, CCC = 0.42). The Animal_VFA equation (Eq. 86) indicated that rumen propionate proportion negatively correlates with CH_4 yield and had a low prediction performance (RMSPE = 20.2%, RSR = 1.03, CCC = 0.32) and higher slope bias than observed for the other equations. The Global equation selected DMI and BW as the only key predictors of the CH_4 yield. The evaluation of these universal equations to predict CH_4 yield across different subsets identified several equations (Eqs. 80, 83, 85 and 86) with lower prediction performances for MD than for FD. Similarly, most equations for predicting CH_4 yield had higher prediction performances when applied to temperate than warm climates.

4. Discussion

4.1. Dry matter and gross energy intake

In line with previous research conducted with sheep (Patra et al., 2016; Swainson et al., 2018), dairy cows (Holter and Young, 1992; Mills et al., 2003; Ramin and Huhtanen, 2013; Niu et al., 2018) and beef cattle (Yan et al., 2009; van Lingen et al., 2019), the current study confirmed that DMI is the most important predictor of enteric CH_4 production as it was positively and highly correlated with CH_4 production across all databases considered. Some studies have found a slightly lower correlation between CH_4 production and DMI than with GEI in sheep (Zhao et al., 2016; Ma et al., 2019), an aspect that was not noted in our study. The inclusion of DMI in all equations during the variable selection process and the low prediction performance of the Animal_no_DMI equation highlighted the relevance of DMI in comparison to other variables. This observation indicates that the more substrate is ingested and available for rumen microbial fermentation, the more enteric CH_4 is emitted (Hristov et al., 2013). In our database, the average CH_4

Table 7
Universal CH_4 yield (g/kg DMI per sheep) prediction equations for various categories and model performance across the data subsets.

Eq.	Category	Prediction equation	n	Subset	Model performance				
					RMSPE	RSR	MB	SB	CCC
[80]	DMI	24.4 (0.546) - 5.24 (0.285) × DMI	2,135	All data	23.5	1.00	3.41	2.04	0.17
			1,374	Adult	22.3	1.04	15.8	1.17	0.19
			761	Young	26.0	0.98	3.32	0.74	0.17
			1,797	FD	22.1	1.00	6.85	1.18	0.19
			338	MD	31.2	1.06	1.92	9.61	0.05
			1,222	Temp.	21.1	0.93	2.18	0.11	0.26
			913	Warm	26.4	1.07	5.13	8.39	0.06
[81]	DMI+BW; Global	19.9 (0.593) - 7.58 (0.354) × DMI + 0.150 (0.0120) × BW	1,810	All data	22.0	0.95	1.05	2.59	0.29
			1,165	Adult	21.7	0.99	1.61	6.39	0.26
			645	Young	22.7	0.91	0.33	0.03	0.28
			1,566	FD	22.1	0.98	1.74	4.27	0.26
			244	MD	21.6	0.83	1.03	2.73	0.43
			905	Temp.	19.9	0.94	1.12	3.63	0.35
			905	Warm	23.9	0.96	7.37	0.33	0.26
[82]	DMI+OMD+BW	18.3 (1.50) - 8.97 (0.468) × DMI + 0.0371 (0.182) × OMD + 0.169 (0.0159) × BW	1,020	All data	19.9	0.87	2.11	0.05	0.42
			716	Adult	18.8	0.86	5.73	0.34	0.47
			304	Young	22.5	0.89	0.28	0.38	0.31
			824	FD	19.9	0.88	4.14	0.06	0.42
			196	MD	19.9	0.83	1.19	0.11	0.47
			333	Temp.	16.1	0.72	0.42	0.03	0.65
			687	Warm	21.3	0.92	4.87	0.03	0.31
[83]	Diet	26.1 (1.55) - 5.39 (0.283) × DMI + 0.323 (0.0500) × ASH - 0.0486 (0.0158) × For	2,135	All data	24.3	1.03	5.94	4.79	0.16
			1,374	Adult	23.1	1.08	23.4	1.03	0.20
			761	Young	26.8	1.01	2.97	4.75	0.17
			1,797	FD	23.0	1.04	11.1	2.99	0.18
			338	MD	31.8	1.08	2.04	13.0	0.08
			1,222	Temp.	22.0	0.97	5.59	0.89	0.25
			913	Warm	27.2	1.10	6.46	11.5	0.05
[84]	Animal	17.6 (0.711) - 7.58 (0.350) × DMI + 0.287 (0.0489) × ASH + 0.147 (0.0119) × BW	1,810	All data	21.6	0.93	0.91	2.13	0.32
			1,165	Adult	21.3	0.98	2.53	4.83	0.29
			645	Young	22.3	0.89	0.06	0.10	0.35
			1,566	FD	21.6	0.96	1.09	3.48	0.30
			244	MD	21.9	0.84	0.11	1.32	0.42
			905	Temp.	19.7	0.93	1.46	3.37	0.37
			905	Warm	23.3	0.94	7.44	0.09	0.30
[85]	Animal_no_DMI	12.0 (1.23) + 0.131 (0.0295) × ADF + 0.413 (0.0611) × ASH	1,810	All data	23.2	1.00	0.27	1.50	0.06
			1,165	Adult	22.6	1.03	3.36	3.39	0.01
			645	Young	24.3	0.97	3.46	0.00	0.15
			1,566	FD	22.6	1.00	0.36	1.04	0.05
			244	MD	27.0	1.03	0.00	6.78	0.01
			905	Temp.	22.3	1.05	0.12	9.81	0.02
			905	Warm	23.9	0.97	0.47	0.36	0.11
[86]	Animal_VFA	30.2 (1.68) - 6.16 (0.889) × DMI - 0.508 (0.0458) × Pro + 0.119 (0.0306) × BW	584	All data	20.2	1.03	1.30	15.8	0.32
			286	Adult	20.2	1.04	12.2	13.5	0.40
			298	Young	20.2	1.03	1.46	12.5	0.26
			468	FD	18.8	1.01	2.04	12.6	0.32
			116	MD	25.5	1.09	0.07	25.3	0.32
			461	Temp.	18.6	1.04	1.06	15.2	0.30
			123	Warm	25.8	1.02	2.21	16.8	0.36

In grey is indicated the database used for model development and evaluation. Equations are presented with regression coefficient standard errors in parenthesis. RMSPE, Root mean square prediction error, expressed as a percentage of observed CH_4 emission means; RSR, RMSPE-observations standard deviation ratio; MB, mean bias as a percentage of MSPE; SB, slope bias as a percentage of MSPE; CCC, Concordance Correlation Coefficient; FD, forage diet (≥95% forage); MD, mixed diet (<95% forage); Temp, temperate climate; Warm, Warm climate; DMI, dry matter intake (kg/d); GEI, gross energy intake (MJ/d); BW, body weight (kg); OMD, organic matter digestibility (%); IPCC, Intergovernmental Panel on Climate Change; For, dietary forage (% DM); ASH, dietary ash (% DM); ADF, dietary acid detergent fibre (% DM); Pro, propionate (%).

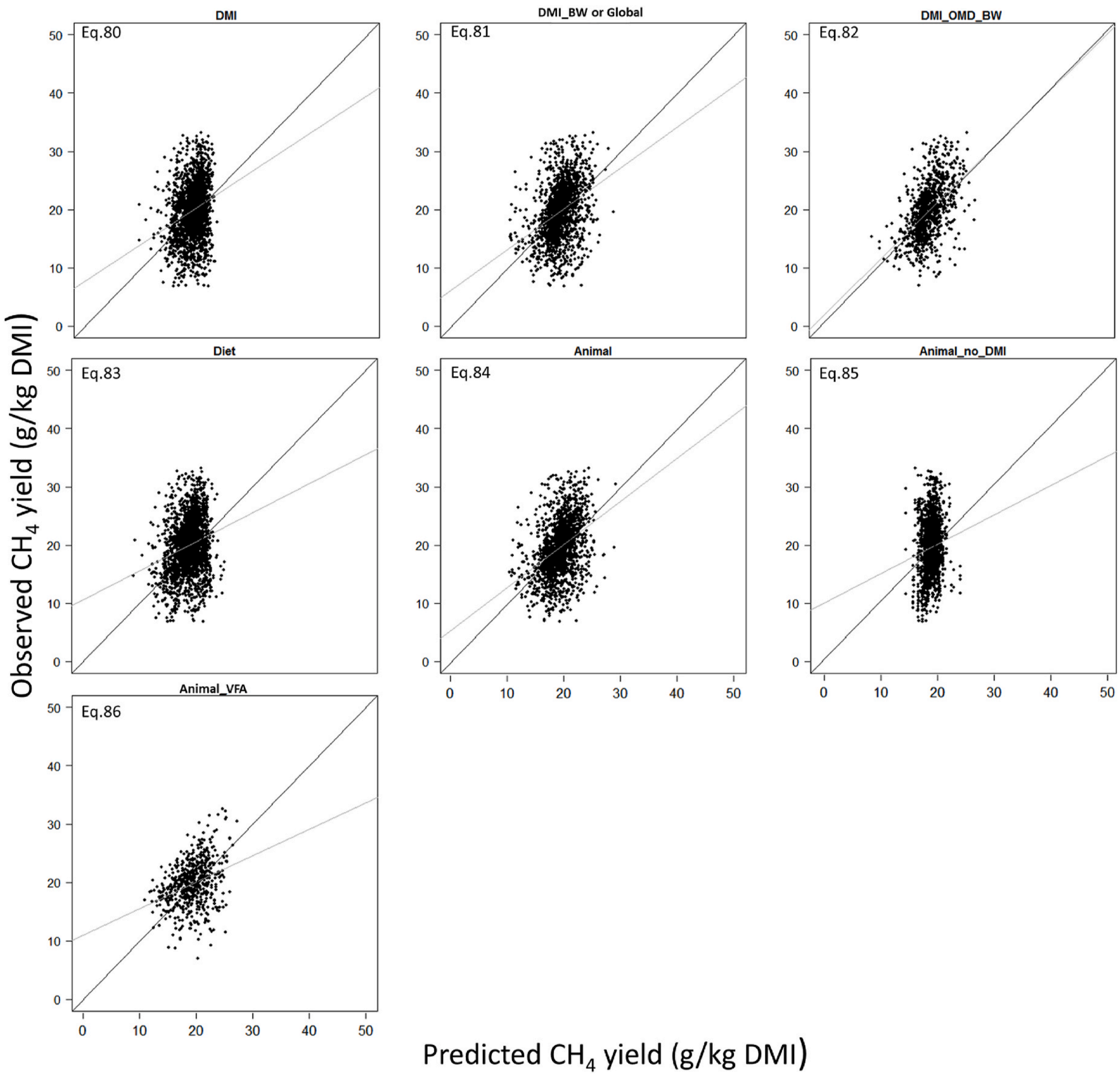

Fig. 3. Observed *vs.* predicted plots for universal CH_4 yield (g/kg DMI per animal) prediction equations at different complexity levels of DMI (Eq. 80), DMI + BW (Eq. 81), DMI + OMD + BW (Eq. 82), Diet (Eq. 83 included DMI and diet composition variables), Animal (Eq. 84 included DMI, diet composition and BW), Animal_no_DMI (Eq. 85 included diet composition and BW), Animal_VFA (Eq. 86 included DMI, rumen VFA and BW) and Global (Eq. 81 included all available variables). The grey and black solid lines represent the fitted regression line for the relationship between the predicted and observed values and the identity line ($y = x$), respectively.

production in sheep was 19.9 g/kg DMI and $Y_m = 6.3\%$, which is similar to that reported by the IPCC 2006 for adult sheep ($Y_m = 6.5\%$), within the range proposed by the IPCC (2019) for dairy cows (5.7–6.5%) and in the upper range for beef cattle (3.0–7.0%). However, Y_m values from the current analysis were slightly lower than the 7.2% reported for sheep (Pelchen and Peters, 1998) or by the latest IPCC guidelines (2019; $Y_m =$ 6.7%), which was mainly derived from measurements using high-forage diets (Swainson et al., 2018). These particularities (adult sheep and forage diets) may explain the lower prediction performance observed for the IPCC equations when applied to young sheep and MD. This observation suggests that the current IPCC 2019 equation can be used for a rough CH_4 estimation. However, the large slope bias noted when the IPCC equation was applied to our database might be due to the lack of intercept (predicted emissions at zero DMI), leading to substantial underestimation and overestimating of CH_4 production at the low and high DMI ends, respectively. The universal DMI (and GEI) equations showed a noticeable intercept (basal CH_4 production) and a slope ranging from 10.3 to 12.8 g of CH_4/kg DMI across the different subsets being 13% lower for young than for adult sheep and 19% lower for MD than for FD. These differences may reflect directly or indirectly the differences in diet composition, as the diets of young sheep and the MD subset diets contained proportionally less forage. Therefore, if a simple approach is required (i.e., one that does not need to take into account the type of diet or BW), the use of a universal DMI equation (Eq. 1) can easily be justified for adult sheep or animals eating FD across different climatic conditions, but not for young sheep or animals eating MD.

The negative correlation between DMI and CH_4 yield (Table 7) is in agreement with previous observations in which the feeding level was evaluated in sheep (Muetzel and Clark, 2015; Patra et al., 2016). Increased intake may potentially increase the passage rate and shorten rumen retention time leading to lower feed digestibility and CH_4 yield in sheep (Blaxter and Clapperton, 1965; Molano and Clark, 2008; Hammond et al., 2013). The high DMI generally observed in lactating sheep (Avondo et al., 2002) could potentially lead to low CH_4 yields; however, the small number of observations with lactating sheep ($n = 66$) in our study precluded the development of robust equations for lactating sheep. The latest update of the IPCC guidelines (2019) aimed to address this problem by suggesting the use of different Y_m values (from 6.5 to

7.0) for different DMI ranges (from <0.6 to >0.8 kg/d). However, using only DMI (or GEI) to predict CH_4 production in sheep does not sufficiently reflect the underlying biology, and further improvements in prediction performance may be achieved using more complex models.

4.2. Body weight

As expected, CH_4 production rose with larger BW (likely as a result of increased DMI), which promotes a substantial increase in the prediction performance when BW is included as a variable in combination with DMI. The positive relationship between BW and CH_4 production noted in most equations (including Animal, Animal_no_diet, Rumen_VFA and Global) across all databases aligns with previous observations in sheep (Pelchen and Peters, 1998; Patra et al., 2016; Swainson et al., 2018) and cattle (Moraes et al., 2014; Escobar-Bahamondes et al., 2017; van Lingen et al., 2019). It has been shown that rumen volume is proportional to the BW of animals (Smith and Baldwin, 1974); therefore, smaller animals ingest less feed and emit less CH_4 (Hristov et al., 2013). This relationship should be particularly considered when estimating CH_4 production in young animals as including BW substantially increased prediction performances. The fact that fast-growing lambs can eat similar amounts of feed as heavier non-growing adults, implies that lambs tend to have higher feeding levels than adult sheep as noted in our study (DMI = 2.8 vs. 2.0% of the BW, respectively). Therefore, it has been hypothesized that at similar DMI, small animals tend to produce less CH_4 as the rumen retention time is shorter due to a greater feeding level based on a higher DMI/BW ratio (Blaxter and Clapperton, 1965; Hammond et al., 2013; Huhtanen et al., 2016). In this context, Goopy et al. (2014) found that naturally low CH_4 yielding sheep also had a smaller rumen size as occurs with lambs. Hence, BW determines to some extent rumen volume and indirectly influences DMI and ruminal passage rate, which ultimately affects feed digestibility, rumen fermentation, CH_4 production and yield. These observations justify the development of specific equations for young and adult sheep as was proposed by several authors (Pelchen and Peters, 1998; Muetzel and Clark, 2015; Swainson et al., 2018; IPCC, 2019). The positive effect of including BW in the equations for MD could be partly explained by the fact that two-thirds of the MD data was related to young sheep.

4.3. Diet composition and digestibility

Equations developed for dairy and beef cattle often show a positive correlation between CH_4 production and dietary NDF, ADF, and/or forage content. This is based on the premise that structural carbohydrates favour acetate production pathway in the rumen resulting in more molecular hydrogen and ultimately CH_4 production (Johnson and Johnson, 1995; Bannink et al., 2011). Fraser et al. (2015) also noted that zero-grazing lambs on extensively managed permanent pasture with high fiber and low sugar content had higher CH_4 yield than those fed cut-and-carry ryegrass indoor due to a higher fiber content. Similarly, dietary lipid content is negatively related to CH_4 production in cattle because of its inhibitory effect on cellulolytic bacteria, protozoa, and NDF digestibility (Grainger and Beauchemin, 2011). Therefore, the overall lack of major effects of diet composition in our models is perhaps surprising since similar prediction performance was noted for the DMI and Diet equations (Eqs. 1 vs 5). Our study database showed that diets consumed by sheep had similar CP (14.8%) but substantially higher NDF content (51.1%) than described in dairy (35.4%, Niu et al., 2018) and beef cattle (35.0%, van Lingen et al., 2019). In this sense, there is consistency in the literature with the lack of a significant influence of diet quality on CH_4 production from temperate grass-based diets in sheep and beef cattle (Molano and Clark, 2008; Hammond et al., 2011; Jonker et al., 2015; Swainson et al., 2018). Van Gastelen et al. (2019) evaluated if dietary strategies are equally effective across dairy cattle, beef cattle and sheep. They concluded that forage related CH_4 mitigation strategies (e.g., by varying NDF content or forage digestibility) were effective for dairy cattle, but had no or minor effects in sheep. Such species differences are in line with the improved prediction performance when including NDF content in models in dairy cattle (Niu et al., 2018) but lack of improved prediction performance in models in sheep, as noted in our study. Similar findings were observed by Pelchen and Peters (1998) in sheep fed various diets suggesting that high fibre content above certain levels can lead to lower feed digestibility and consequently decreased DMI and CH_4 production, as noted in some of our equations (Eqs. 16, 18 and 42). A modelling study also predicted that a decrease in CH_4 yield with increasing concentrate is only observed for dietary forage contents below 65% (Sauvant and Giger-Reverdin, 2009). In our database, only 4% of the animals were fed less than 65% of forage and a negative correlation was observed between dietary NDF content and OMD ($r = 0.34$), both of which can justify the low predictive ability of nutritional composition of the diet on CH_4 production. Moreover, the fact that sheep diets generally have lower and relatively constant EE content than those reported for beef (van Lingen et al., 2019) and dairy cattle (Niu et al., 2018) may explain the low predictive power of the EE variable in our database. Similar to our models, previous models also excluded EE concentration from the CH_4 prediction models for cattle (Moraes et al., 2014) and sheep (Patra et al., 2016). On the contrary, ash content showed a positive association with CH_4 production in several equations (Eqs. 5, 6, 7, 29, 40, 41, 74 and 75), possibly because ash content was positively correlated with forage content ($r = 0.31$) as preserved forages consumed by sheep had higher ash concentration (8.58%) than observed in dairy (7.3%, Niu et al., 2018) and beef cattle (6.29%, van Lingen et al., 2019). In contrast to cattle, sheep hardly ever are fed on total mixed rations (TMR) and have a higher feed selection capacity. Both factors can lead to a higher uncertainty concerning the actual nutritional composition of the feed ingested by sheep and the subsequent prediction equations.

Our study showed that OMD was positively associated with CH_4 production (Eq. 4) and CH_4 yield (Eq. 61) in the universal DMI + OMD + BW equations. This was expected as greater amounts of fermentable feed in the rumen produce more hydrogen for CH_4 production by methanogens (Moss et al., 2000; Ramin and Huhtanen, 2013). As a result, Muetzel and Clark (2015) reported that OMD in addition to DMI can explain up to 84% of the CH_4 production in grazing sheep. However, Pelchen and Peters (1998) indicated that the increase in CH_4 production by increased digestibility only applies to OMD below a certain threshold (around 72%), whereas a negative correlation can appear at higher OMD values as a result of lower NDF content and/or higher feeding level (Swainson et al., 2018). Despite these complex associative effects between diet composition and rumen physiology, the IPCC (2019) guidelines recommend using lower Y_m values for higher digestibility (and lower NDF content) in dairy cows and beef cattle but not in sheep. Our study showed that this concept could also be applied to sheep since the DMI + OMD + BW equation provided the best prediction performance across all universal CH_4 production CH_4 yield models.

4.4. Rumen fermentation

Despite several meta-analyses have described an association between rumen protozoa on enteric CH_4 production (Guyader et al., 2014; Newbold et al., 2015), to our knowledge, this is the first study that investigated the inclusion of rumen fermentation-related variables into the enteric CH_4 prediction equations in sheep using a large international database. It has been hypothesized that a low rumen pH can decrease Y_m (Van Kessel and Russell, 1996; Lana et al., 1998) because it is often associated with the fermentation of non-structural carbohydrates and inhibition of microbes involved in rumen methanogenesis including protozoa (acting as hydrogen producers) and methanogens. Similarly, a low total VFA concentration in the rumen is generally associated with low substrate fermentation and low CH_4 production (Brask et al., 2015). However, Swainson et al. (2018) indicated that the availability of fermentable substrates dominates any negative pH effect on CH_4

production in sheep. Moreover, these rumen variables are highly affected by the diurnal cycles and sampling time, an aspect that could explain the lack of significant associations with daily CH_4 production (Jonker et al., 2019) as noted in our study.

Compared to rumen pH and total VFA concentration, the molar proportions of individual VFA tend to remain more constant (Belanche et al., 2012; Brask et al., 2015). It is widely accepted that the rumen fermentation pattern of the diet determines hydrogen production which is ultimately used to produce CH_4. High propionate production is associated with lower hydrogen release and CH_4 production, whereas high acetate production (and butyrate to a lower extent) are related to higher CH4 production according to the classical thermodynamics of NADH oxidation in anaerobic microbial fermentation (Van Lingen et al., 2016). Although VFA production and their rumen concentrations are not always proportional due to the differential absorption rates (Noziere et al., 2011), our equations showed that propionate molar proportion had a consistent and negative association with CH_4 production (Eqs. 8, 19, 20, 43, 44 and 54), whereas the opposite was true for acetate and butyrate molar proportions (Eqs. 9, 31, 32, 55 and 66). The selection of the VFA molar proportions in the Rumen_VFA and Global universal models highlights the relevance of these variables leading to improved prediction performances than reported for DMI or Diet equations. Jonker et al. (2015) observed similar correlation coefficients to our study between CH_4 production and molar proportion of propionate ($r = -0.82$) in sheep fed fresh pasture, but they also observed a similar correlation with acetate to propionate ratio ($r = 0.82$). In our study, the acetate to propionate ratio was not selected by any prediction equation for CH_4 production or yield, possibly because of the high diversity of diets, metabolic pathways and fermentation products. These findings suggest that rumen VFA data could be used (if available) in adult sheep models, but not in the universal models since they did not outperform the DMI + OMD + BW equation. Moreover, the universal equations including VFA molar proportions had a substantially lower prediction performance for young than for adult sheep, which justifies the development of age-specific equations as discussed below. The use of rumen fermentation data may not be practical on farm conditions or for national inventories, but could represent an opportunity to improve CH_4 predictions for more refined studies when rumen fluid is available from research animals or abattoirs.

4.5. Age-specific equations

Using age-specific equations was initially applied by the IPCC (2006), suggesting higher Y_m values for adult sheep than for young (post-weaned) sheep based on New Zealand studies in which DMI was estimated using digesta markers and CH_4 production was measured using SF_6 in grazing systems. Moreover, the growth rate of young stock represents an important energy sink which often leads to lower enteric CH_4 yields and emission intensities (Niu et al., 2018). A meta-analysis of CH_4 production from sheep < 1-year and those > 1-year-old suggested that production between these age categories are different for the same level of intake (Muetzel and Clark, 2015). However, more recent studies (Swainson et al., 2018) suggested that the differences in Y_m between age groups were negligible, which is also reflected in the current IPCC 2019 guidelines (common Y_m of 6.7% for all sheep). In our study an average Y_m of 6.59 and 5.86% was observed for adult sheep and young (post-weaned) sheep respectively, suggesting that the difference between the two groups is somewhat smaller than indicated in the previous IPCC 2006 guidelines (6.5 and 4.5%, respectively). Therefore, this study mostly supports and expands the IPCC (2006) approach since the adult sheep equation based on DMI (Eq. 13), in comparison to the young sheep equation (Eq. 24), had a higher intercept (7.82 vs. 5.63) and higher slope (12.7 vs 11.0 g CH_4/d), indicating greater Y_m for adult than for young sheep as previously noted (Muetzel and Clark, 2015). These findings suggest the resumption of age-specific equations in future IPCC guidelines to increase CH_4 prediction performances.

The adult sheep equations showed an overall high prediction accuracy which was not considerably affected across diets or climate regions. The adult-sheep Animal_VFA (Eq. 19 based on DMI and propionate) and the Global equations (Eq. 20 based on DMI, propionate and ADF) showed the most promising results based on the inclusion of DMI and rumen propionate proportion as key variables. On the contrary, BW was not selected as a relevant prediction variable for adult sheep as a weak correlation between BW and CH_4 (and between BW and DMI) has been reported in adult sheep from different breeds (Moorby et al., 2015). These results need further confirmation, because the number of observations used to evaluate equations containing rumen parameter was much smaller ($n = 286$) than most other equations (n = 1,374). These new equations could represent a step change for a more accurate estimation of CH_4 production in research groups that have access to rumen fermentation data through rumen fistula intubation but are unable to perform direct CH_4 measurements. Oro-gastric intubation or rumen sampling after slaughter could potentially represent alternative methods to obtain rumen fermentation data to be implemented in these prediction equations (Ramos-Morales et al., 2014). Alternatively, the most simplistic adult-sheep DMI or GEI equations (Eq. 13 and 14) could be also successfully used to predict CH_4 production in farm conditions (or for national inventories) where rumen VFA data are not available.

On the contrary, the young-sheep equations tended to have lower prediction performance than those for adult sheep but had similar performance as the universal equations applied to young sheep. The limited size of the young sheep database and the high diversity of feeds and production systems may explain these results. Therefore, the universal equation DMI + BW (Eq. 3) could be considered as the best applicable equation for predicting CH_4 production in young sheep, given that these variables are able to be monitored on-farm, and due to its higher prediction performance than the extant IPCC (2019) equations. Alternatively, more complex universal equations such as DMI + OMD + BW (Eq. 4) or Diet (Eq. 6) led to similar predictions than to the equivalent universal equations when applied to young sheep. These findings suggest that when estimating CH_4 production in young sheep, BW is more relevant than diet composition as previously suggested (Muetzel and Clark, 2015). These findings suggest that these equations can be used to predict individual emissions from single animals. Alternatively, if the group average DMI and BW are known, CH_4 production by sheep can also be predicted for a herd, area or country, opening the possibility to be implemented by a wide range of users. These users could be interested in assessing the global or national emissions (e.g. environmental agencies and policy-makers), the environmental footprint of sheep products (e.g. producers, farmer's cooperatives, extension services, retailers, marketing companies and consumers) or to evaluate the effectiveness of CH_4 mitigation strategies (e.g. researchers and farm advisers).

4.6. Diet-specific equations

The concept of developing specific equations for diets with different forage proportions has been explored in previous works on beef and dairy cattle (Niu et al., 2018; van Lingen et al., 2019). As a result, the IPCC guidelines (2019) suggest the use of a gradient of Y_m values from 5.7 to 6.5 for dairy cattle and buffalo diets with DM digestibility values between >70% and <62%, and from 3.0 to 7.0 for non-dairy and multipurpose cattle and buffalo diets with digestibility values between >75% and <62%, respectively. Considering the small amount of forage generally used in feedlot diets for beef cattle, Van Lingen et al. (2019) suggested using different equations for animals fed either <18% or >25% of forage. However, the diets used in beef cattle had a much lower proportion of forage (mean 51.0%, van Lingen et al., 2019) than our sheep database (mean 95.8%) and a large proportion of the sheep data (84%) were essentially obtained from only-forage diets, which justified the development of specific equations for FD and for MD.

The FD-specific equations derived from our database marginally increased the CH_4 prediction performance compared to their equivalent universal equations, possibly because most of the observations in the entire database corresponded to FD. This observation supports the general use of complex universal equations such Animal (Eq. 6) or Animal_VFA (Eq. 8). Alternatively, simpler FD-specific equations including DMI (Eq. 36), GEI (Eq. 37) or DMI + BW (Eq. 38) as key variables led to similar prediction performances but with lower systematic bias, thus making them more reliable and practical. A similar selection of variables (DMI, BW, and forage proportion) was proposed by Van Lingen et al. (2019) for beef cattle fed high-forage diets. The experiment of Savian et al. (2014) indicated that other factors such as the grazing intensity and stocking method can have a high impact on CH_4 intensity in grazing sheep.

Our findings also suggest that MD-specific equations only lead to modest prediction performances of CH_4 production, and the results should be carefully interpreted given the relatively small number of observations in the database. The use of DMI or GEI (Eqs. 48 and 49) as a single variable led to inaccurate CH_4 estimates, and the inclusion of BW is highly recommended in order to increase prediction performance (Eqs. 50, 51 and 52). These results disagree with those of Ellis et al. (2009) who identified DMI and NDF/starch ratio (but not BW) as the key variables to predict CH_4 production in beef cattle fed mixed diets. Most MD-specific equations did not outperform the universal equations when applied to animals fed MD. As a result, the universal equation which includes DMI + BW and DMI + BW + OMD (Eqs. 3 and 4) should be recommended to predict CH_4 production in sheep fed MD, with the understanding that its high slope bias could potentially lead to substantial errors when extrapolated to extreme values. These observations suggest that appropriate universal equations can adequately be applied to different types of diets without compromising CH_4 prediction performance.

4.7. Climatic region-specific equations

The concept of developing region-specific equations has previously been explored on the basis that different diets, and forages of different type and quality, are used across different regions. As a result, specific equations have been developed for Europe and North America for dairy (Niu et al., 2018) and beef cattle (van Lingen et al., 2019). In this study, regions were classified based on the climate due to the large geographical diversity observed in our intercontinental database. The higher CH_4 production observed in the warm-climate database (+14.5%) could be explained by the greater DMI (+12.5%) and dietary NDF (+8.7%) than that observed in the temperate-climate database. Despite these differences, the universal equations were able to predict CH_4 production across both climatic regions. For temperate-climatic regions the most effective prediction was achieved by the universal Animal_VFA (Eq. 8 including DMI, propionate and BW) and by the region-specific Animal equation (Eq. 64 including DMI, EE, For and BW). For warm-climatic regions, the lowest prediction error was achieved by the DMI + BW and DMI + OMD + BW equations, with a slightly higher prediction performance and lower slope bias when they were region-specific (Eqs. 72 and 73), rather than universal equations (Eqs. 3 and 4). Zubieta et al. (2021) showed that the CH_4 intensity derived from growing ruminants grazing high quality forages (i.e. temperate and tropical forages) can become similar to those on nutrient-dense diets in feedlots if grazing management is optimal. These findings support similar results observed in beef cattle (van Lingen et al., 2019) and suggest that enteric CH_4 prediction models developed in an intercontinental context had similar performance across climatic regions.

5. Conclusions

Dry matter intake is the key variable for predicting enteric CH_4 production in sheep. However, increasing the model complexity by including BW, OMD or rumen propionate proportion improved prediction performances for the universal equations, whereas diet composition had a minor impact. Prediction performance was increased through developing age-specific models to accommodate the physiological and dietary differences. For adult sheep (>1-year-old), models should include DMI alone or in combination with propionate molar proportion as the key variables. On the contrary, for young sheep (<1-year-old), the universal models can be applied if DMI and BW are included as key variables. Our findings indicate that appropriate universal equations accurately predict CH_4 production across different diets and climatic conditions without compromising prediction performance. The equations developed in the present study commonly had lower prediction errors than the extant IPCC 2019 equations. Equations for CH_4 yield led to low prediction performances, with DMI being negatively and BW and OMD positively correlated with CH_4 yield. These findings suggest that the proposed universal equations, in combination with the age-specific equations represent an opportunity to improve ovine CH_4 production estimates in national or global inventories and for research purposes.

CRediT authorship contribution statement

Alejandro Belanche: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Alexander N. Hristov:** Conceptualization, Writing – review & editing. **Henk J. van Lingen:** Conceptualization, Methodology, Writing – review & editing. **Stuart E. Denman:** Conceptualization, Writing – review & editing. **Ermias Kebreab:** Conceptualization, Writing – review & editing. **Angela Schwarm:** Conceptualization, Writing – review & editing. **Michael Kreuzer:** Conceptualization, Writing – review & editing. **Mutian Niu:** Conceptualization, Writing – review & editing. **Maguy Eugène:** Conceptualization, Writing – review & editing. **Vincent Niderkorn:** Conceptualization, Writing – review & editing. **Cécile Martin:** Conceptualization, Writing – review & editing. **Harry Archimède:** Conceptualization, Writing – review & editing. **Mark McGee:** Conceptualization, Writing – review & editing. **Christopher K. Reynolds:** Conceptualization, Writing – review & editing. **Les A. Crompton:** Conceptualization, Writing – review & editing. **Ali Reza Bayat:** Conceptualization, Writing – review & editing. **Zhongtang Yu:** Conceptualization, Writing – review & editing. **André Bannink:** Conceptualization, Writing – review & editing. **Jan Dijkstra:** Conceptualization, Writing – review & editing. **Alex V. Chaves:** Conceptualization, Writing – review & editing. **Harry Clark:** Conceptualization, Writing – review & editing. **Stefan Muetzel:** Conceptualization, Writing – review & editing. **Vibeke Lind:** Conceptualization, Writing – review & editing. **Jon M. Moorby:** Conceptualization, Writing – review & editing. **John A. Rooke:** Conceptualization, Writing – review & editing. **Aurélie Aubry:** Conceptualization, Writing – review & editing. **Walter Antezana:** Conceptualization, Writing – review & editing. **Min Wang:** Conceptualization, Writing – review & editing. **Roger Hegarty:** Conceptualization, Writing – review & editing. **V. Hutton Oddy:** Conceptualization, Writing – review & editing. **Julian Hill:** Conceptualization, Writing – review & editing. **Philip E. Vercoe:** Conceptualization, Writing – review & editing. **Jean Víctor Savian:** Conceptualization, Writing – review & editing. **Adibe Luiz Abdalla:** Conceptualization, Writing – review & editing. **Yosra A. Soltan:** Conceptualization, Writing – review & editing. **Alda Lúcia Gomes Monteiro:** Conceptualization, Writing – review & editing. **Juan Carlos Ku-Vera:** Conceptualization, Writing – review & editing. **Gustavo Jaurena:** Conceptualization, Writing – review & editing. **Carlos A. Gómez-Bravo:** Conceptualization, Writing – review & editing. **Olga L. Mayorga:** Conceptualization, Writing – review & editing. **Guilhermo F. S. Congio:** Conceptualization, Writing – review & editing. **David R. Yáñez-Ruiz:** Funding acquisition, Data curation, Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jclepro.2022.135523.

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