Mitig Adapt Strateg Glob Change (2017) 22:629–650
DOI 10.1007/s11027-015-9691-7

ORIGINAL ARTICLE

Prediction of enteric methane emission from cattle using linear and non-linear statistical models in tropical production systems

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Received: 16 July 2015 / Accepted: 27 October 2015 / Published online: 30 November 2015

Abstract The objective of this study was to develop linear and nonlinear statistical models to predict enteric methane emission (EME) from cattle (Bos) in the tropics based on dietary and animal characteristic variables. A database from 35 publications, which included 142 mean observations of EME measured on 830 cattle, was constructed to develop EME prediction models. Several extant equations of EME developed for North American and European cattle were also evaluated for suitability of those equations in this dataset. The average feed intake and methane production were 7.7±0.34 kg/day and 7.99±0.39 MJ/day, respectively. The simple linear equation that predicted EME with high precision and accuracy was: methane (MJ/day)=$1.29_{(\pm 0.906)}+0.878_{(\pm 0.125)}\times$dry matter intake (DMI, kg/day), [root mean square prediction error (RMSPE)=31.0 % with 92 % of RMSPE being random error; R^2=0.70]. Multiple regression equation that predicted methane production slightly better than simple prediction equations was: methane (MJ/day)=$0.910_{(\pm 0.746)}+1.472_{(\pm 0.154)}\times$DMI (kg/day) – $1.388_{(\pm 0.451)}\times$feeding level as a multiple of maintenace energy intake – $0.669_{(\pm 0.338)}\times$acid detergent fiber intake (kg/day), [RMSPE=22.2 %, with 99.6 % of MSPE from random error; R^2=0.84]. Among the nonlinear equations developed, Mitscherlich model, i.e., methane (MJ/day)=$71.47_{(\pm 22.14.6)}\times$(1 - exp{$-0.0156_{(\pm 0.0051)}\times$DMI (kg/day), [RMSPE=30.3 %, with 97.6 % of RMSPE from random error; R^2=0.83] performed better than simple linear and other nonlinear models, but the predictability and goodness of fits of the equation did not improve compared with the multiple regression models. Extant equations overestimated EME, and many extant models had low accuracy and precision. The equations developed in this study will be useful for improved estimates of national methane inventory preparation and for a better understanding of dietary factors influencing EME for tropical cattle feeding systems.

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Keyword Cattle · Enteric methane production · Nutrient intake · Tropical production · Statistical model

1 Introduction

Methane (CH4) production from the fermentation of feeds in the rumen represents a loss of up to 15 % of the gross energy (GE) intake depending upon the type of diets (Holter and Young 1992). Moreover, livestock production systems contribute a substantial share of greenhouse gases (GHG) to the atmosphere with an estimate of 7.1 gigatonnes (in CO_2 equivalent) annually representing 14.5 % of total anthropogenic GHG (Gerber et al. 2013), and methane production from enteric fermentation represents about 40 % of total GHG emissions from livestock production systems (Gerber et al. 2013; Patra 2012, 2014a). For these purposes, several models had been developed since many years for predicting methane production and a better understanding of the dietary factors affecting this rumen fermentation process (e.g., Kriss 1930; Ramin and Huhtanen 2013; Patra and Lalhriatpuii 2016). However, all the models of prediction of methane production in cattle (Bos) were developed for North American and European temperate livestock production systems, and thus, the parameter estimates are more related to cattle raised in those regions.

Based on the data of Food and Agricultural Organization (http://faostat3.fao.org, accessed 24 October. 2015), more than 60 % of the global cattle populations are located in the tropical regions of the world, where animal production systems are markedly different from temperate livestock production. Basal feeds for ruminants in tropical environments are predominantly of low quality high fibrous forages (Van Soest 1994). Breeds of livestock species in the tropics also greatly differ from temperate regions, which may also differ for rumen function and digestive efficiency (Hegarty 2004). Several studies indicated that methane production, diversity, and abundances of methanogens in ruminants may vary depending upon diets (Bouchard et al. 2013; Hammond et al. 2013) and breeds (Hernandez-Sanabria et al. 2013; King et al. 2011; Zhou et al. 2010). Despite the considerable differences in feed composition and production systems between tropics and temperate environments, prediction models of methane emissions in cattle from tropical production systems have not been developed from a large data base spanning over wide variety of diets. Moreover, GHG emissions from livestock populations of the developing tropical regions are expected to grow increasingly in the years ahead due to expanding livestock populations (Gerber et al. 2013; Patra 2014a). Development of enteric methane prediction models is, therefore, required to improve estimates of methane outputs in tropical feeding systems.

Methane gas has high global warming potential (28 times greater than CO_2), but short lifetime (12 years) in the atmosphere (IPCC 2013). Thus, addressing methane emissions is now considered as a quick and immediate mitigation strategy compared with other gases (IPCC 2013). Several mitigation options and technologies are suggested to decrease enteric methane production in ruminants, of which dietary strategies appear to be the most promising options (Hristov et al. 2013). A better understanding of the dietary composition influencing methane production would be useful for mitigation of methane production in tropical feeding conditions. The modelling approach is an effective tool to assess the effectiveness of different nutritional strategies to reduce methane production from ruminants (Benchaar et al. 2001).

A number of empirical and mechanistic models were developed for predicting methane emission from the studies or database of temperate cattle and sheep (Ovis) production (e.g., Blaxter and Clapperton 1965; Moe and Tyrrell 1979; Kebreab et al. 2008; Ramin and Huhtanen

2013). Statistical models predict methane production from nutrient intake, composition, feeding levels, and digestibility directly, while dynamic mechanistic models estimate methane emission using mathematical descriptions of rumen fermentation biochemistry (e.g., Benchaar et al. 2001; Mills et al. 2001; Kebreab et al. 2006; Ellis et al. 2007) and require complex data that are not available routinely. These models are useful to predict enteric methane emission from cattle without undertaking extensive and costly experiments and to explain the dietary factors exerting methane production. Therefore, the objectives of this study were to develop statistical models for prediction of enteric methane emissions for tropical cattle production systems using commonly measured dietary and animal variables and to compare these models with the extant methane prediction models developed for temperate cattle-rearing systems. The models also identified major dietary factors influencing methane production in tropical cattle production systems, which could be useful for nutritional mitigation of methane production.

2 Materials and methods

2.1 Construction of database

A database was compiled from the studies published in journals and conference proceedings for development of methane prediction models. Criteria for inclusion of studies in the database were that the studies provided in vivo methane production from tropical cattle description of the animals and intakes of dry matter (DM) and other nutrients. Overall, 35 publications (Bairagi and Mohini 2003; Bhar et al. 1999; De et al. 2012; Demarchi et al. 2003; Ghosh et al. 2001; Girdhar et al. 1995; Haque et al. 2001; Hulshof et al. 2012; Jain et al. 2011; Kannan and Garg 2009; Kannan et al. 2010; Kannan et al. 2011; Kennedy and Charmley 2012; Kurihara et al. 1999; Lal et al. 1987; Mohini and Mani 2007; Mohini et al. 2007; Malik and Singal 2008; Mohini et al. 2009; Mohini and Singh 2010; Mupeta et al. 2000; Nascimento et al. 2008; Neto et al. 2009; Oliveira et al. 2007; Pattanaik et al. 2003; Pedreira et al. 2009; Pedreira et al. 2012; Pedreira et al. 2013; Perna et al. 2013; Possenti et al. 2008; Primavesi et al. 2003; Primavesi et al. 2004; Rejil et al. 2008; Srivastava and Garg 2002; Tomkins et al. 2011) fulfilled the criteria for inclusion in this database. The studies in these publications were conducted in India (n=19), tropical parts of Brazil (n=12), and Australia (n=3). One study from Zimbabwe was included in this database. There were many studies available from Australia, but studies conducted on tropical forage diets as stated in the publications were only considered in this database. Methane production was measured using either the sulphur hexafluoride (SF_6) technique (n=109) or respiration chamber (n=40). Methane production measured by SF_6 technique and respiration chamber study was 19.1 ±6.66 versus 19.1±4.50 g/kg DM intake and 5.81±1.72 versus 5.93±1.48 percent of GE intake, respectively, in this database. There were a total of 149 treatment means obtained from 830 observations from dairy and beef cattle. However, treatments (n=7) containing feed additives with antimethanogenic properties were removed before statistical analyses.

The investigated dietary and animal factors (independent variables) were body weight (BW), intakes of DM, individual nutrients, GE and metabolizable energy (ME), organic matter and GE digestibility, nutrient composition of diets, forage proportion, and feeding level, which were used for regression equation development. Feeding level (FL) as multiple of maintenance was estimated by dividing the ME intake by the maintenance ME requirement for cattle in tropical countries (Kearl 1982). Because digestibility of nutrients changes with level of feeding, digestibility at maintenance level of feeding is the most consistent assessment of digestibility of feeds (Ramin and Huhtanen 2013). Thus, organic matter digestibility (g/kg) at a maintenance level of feeding (OMDm) was used as a predictor of methane production in this study and was determined using the equation as per Ramin and Huhtanen (2013). Digestibility of OM was estimated from the digestibility of DM when a study did not report OM digestibility using the equation derived from the data in this study. Since few variables were not available across all observations in the data set, the number of observations used for development of prediction equations varied between dietary and response variables depending on the regressor variables available. Data reported in differing units of measurements were transformed to the same units. Some records were incomplete or not reported uniformly, which necessitated the calculations (for example, conversion of methane production in L/day or kcal/day to g/day (1 L=0.714 g methane; 1 L methane=39.75 kJ energy), energy intake in kcal to MJ (1 kcal=4.184 kJ), total digestible nutrients (TDN) value to ME (1 kg TDN=3.6 MJ ME), etc. using standard conversion factors) from the reported data. Whenever possible, missing chemical composition of the diets was calculated from publications included in this dataset with similar ingredients. When a study did not report all possible outcomes and it was not possible to calculate from the reported data, missing variables were considered as missing data.

2.2 Statistical analysis

2.2.1 Linear and binomial model

Statistical analysis procedure used for prediction of methane production from this database was described elsewhere (Patra 2010, 2011). In brief, since studies represented random samples of larger population of studies, methane prediction equations were developed taking into account of the random effect of the study (St-Pierre 2001), using PROC MIXED (SAS 2001) with the following model:

$$\mathrm{Y}_{ij} = \mathrm{B}_0 + \mathrm{B}_1\mathrm{X}_{ij} + \mathrm{B}_2\mathrm{X}_{ij}^2 + \mathrm{s}_i + \mathrm{b}_i\mathrm{X}_{ij} + \mathrm{e}_{ij}$$

Where:

Y_{ij}=the predicted methane production at the level j of the independent variable X in the study i; B_0=the intercept across all studies (fixed effect); B_1 and B_2=the linear and quadratic regressing coefficient of Y on X, respectively, across all studies (fixed effect); X_{ij}=the value j of the variable X in study i; s_i=the random study effect on the intercept; b_i=the random study effect on regression coefficient of X; and e_{ij}=the unexplained residual error.

The observed methane production data were weighted by the number of animals in each study to take into consideration of unequal variance among studies. The slopes and intercepts by study were included as random effects, and an unstructured variance-covariance matrix or a variance component of variance-covariance structure (when a random covariance component was not significant and a model failed to converge) was performed at the random part of the model (St-Pierre 2001). If random covariance or random slope and squared term of predictors were not significant ($P > 0.10$), they were removed from the models. All predictors of methane outputs and their quadratic term were further used to develop multiple regression equations employing the backward elimination multiple regression procedure following the algorithm reported by Oldick et al. (1999) and Patra (2010):

$$\mathrm{Y}_{ij} = \mathrm{B}_0 + \mathrm{B}_{l1}\mathrm{X}_{1ij} + \mathrm{B}_{q2}\mathrm{X}_{1ij}^2 + \mathrm{s}_i + \mathrm{b}_i\mathrm{X}_{ij} + \mathrm{B}_{l2}\mathrm{X}_{ij} + \mathrm{B}_{q2}\mathrm{X}_{ij}^2 \ldots\ldots\ldots + \mathrm{B}_{ln}\mathrm{X}_{\mathrm{nij}}^2 + \mathrm{e}_{ij}$$

where: Y_{ij}=the predicted methane production at the level j of the independent variables $X_1, X_2 \ldots X_n$ in the study i; B_0=the intercept across all studies (fixed effect); B_{l1}, $B_{l2}..B_{ln}$=the linear and B_{q1}, $B_{q2}..B_{qn}$=quadratic regression coefficients of Y on X variables, respectively, across all studies (fixed effect); s_i=the random effect of study i; b_i=the random effect of study i on the regression coefficient of Y on X variables in study i; and e_{ij}=the unexplained residual error. Two-way interactions were added when the coefficients of first order of Xs were significant ($P<0.05$). To evaluate collinearities, a variance inflation factor (VIF) of less than 20 for every continuous independent variable tested was assumed. As the main objective of the study was to predict methane emission from dietary variables, high VIF considered here is not a serious problem (Geary 1963). Because model containing two-way interaction effect resulted in VIF of greater than 20, the interaction effect was not included in any final models. The best-fit equations of multiple regression equations that further improved the relationship obtained from simple linear or polynomial regression are presented. All statistical computations were carried out using the PROC MIXED and PROC CORR procedures of the SAS (2001) software system.

2.2.2 Nonlinear models

Since DM intake as sole independent variable predicted methane emission with highest degree of determination in the linear model, the nonlinear models were developed using DM intake as a determinant for prediction of methane outputs, if prediction ability of the equations could be further improved. The non-linear models employed the relationships exhibiting diminishing returns (monomolecular), sigmoidal (Gompertz), and exponential behaviors. The PROC NLMIXED of SAS was used to parameterize the non-linear functions with a little modification of the equation used by Schulin-Zeuthen et al. (2007) and the exponential model in the following forms:

Monomolecular: $Y=a-(a+b)\times\exp(-c\times x)$
Mitscherlich: $Y=a\times(1-\exp(-c\times x))$
Gompertz: $Y=b\times\exp((1-\exp(-c\times x)\times\ln(a+2b)/b)-2b)$
Exponential: $Y=b\times\exp(c\times x)$
Power: $Y=b\times x^c$

Where Y represents the predicted methane production, the parameters a and b represent the upper asymptote and Y intercept of the nonlinear models, respectively, and c determines the shape of the response curve in the nonlinear functions. Study including parameters a, b, and c was considered random in the models (Schinckel and Craig 2002; Schulin-Zeuthen et al. 2007). The lowest value of Bayesian information criteria (BIC, a measure of regression fit) and biological relevance of the parameters estimated was considered to find out the optimum non-linear models.

2.3 Model evaluation

Predictive abilities of a range of existing models [Kriss (1930), Axelsson (1949), Mills et al. (2003), IPCC (2006) tier II, Ellis et al. (2007), Yan et al. (2009) and Ramin and Huhtanen (2012, 2013)] that were developed for dairy and beef cattle in temperate breeds and feeding situations were compared using inputs from this databases (Table 1). These equations were selected for comparison because they were commonly evaluated in different studies, and their input variables were available from this compiled database. Equations developed in this study

Table 1 List of extant equations used to predict methane production from cattle

Source	Equation
Kriss (1930)	Methane (MJ/day)=0.996+1.246×DM intake (kg/day)
Axelsson (1949)	Methane (MJ/day)=−2.067+2.636×DM intake (kg/day)−0.105×DM intake $(kg/day)^2$
Mills et al. (2003)	Methane (MJ/day)=5.93+0.92×DM intake (kg/day)
	Methane (MJ/day)=8.25+0.07×ME intake (MJ/day)
	Methane (MJ/day)=56.27−(56.27+0)×exp[−0.028×DM intake (kg/day)]
IPCC (2006)	Methane (MJ/day)=0.065×GE intake (MJ/day)
Ellis et al. (2007)	Methane (MJ/day)=3.272+0.736×DM intake (kg/day)
	Methane (MJ/day)=3.63+0.0549×ME intake (MJ/day)+0.606×ADF intake (kg/day)
Yan et al. (2009)	Methane (MJ/day)=0.582+1.40×DM intake (kg/day)
Ramin and Huhtanen (2013)	Methane (MJ/day)=0.797+ 1.427×DM intake (kg/day) − 0.020×DM intake $(kg/day)^2$
	Methane (L/day)=−64+26×DM intake (kg/day) −0.61×cDM intake $(kg/day)^2$+0.25×OMDm (g/kg)−66.4×EE intake (kg/day) − 45×NFC/(NFC+NDF)
Ramin and Huhtanen (2012)	Methane (L/day)=976×[(1−exp (−0.0407×DM intake (kg/day))]
Patra (2014b)	Methane (MJ/day)=1.29+0.788×DM intake (kg/day)
Monomolecular	Methane (MJ/day)=$39.88_{(\pm 17.23)}$×(1 − exp{−$0.0276_{(\pm 0.0132)}$×DM intake (kg/day)}

ADF acid detergent fiber, *DM* dry matter, *ME* metabolizable energy, *GE* gross energy intake, *OMDm* organic matter digestibility determined at a maintenance level of feeding, *EE* ether extract, *NDF* neutral detergent fiber, *NFC* non-fiber carbohydrate

cDM intake=centered DM intake centered, i.e., mean DM intake is subtracted from each DM intake value

and extant equations were compared using mean square prediction error (MSPE), square root of MSPE (RMSPE) expressed as a percentage of the observed mean (Theil 1966), and coefficient of determination (R^2) (Draper and Smith 1998). The MSPE value was calculated as:

$$\mathrm{MSPE} = \sum_{i=1}^{n} (O_i - P_i)^2 \Big/ n$$

where O_i is the observed value for the ith observation, P_i is the predicted value for the ith observation, and n is the number of observations. The RMSPE value, which provides an estimate of the overall prediction error, was expressed as a proportion (RMSPE divided by the observed mean) of the observed mean so that comparisons of RMSPE (%) values can be made among equations with different predicted means and so that deviation from observed values can be evaluated. The MSPE value was decomposed into mean bias or error in central tendency (ECT), slope bias or error due to regression (ER), and random or error due to disturbance (ED). These 3 fractions were calculated as follows (Bibby and Toutenburg 1977):

$$\mathrm{ECT} = \left(\overline{P} - \overline{O}\right)^2$$

$$\mathrm{ER} = \left(S_p - r \times S_0\right)^2$$

$$\mathrm{ED} = \left(1 - r^2\right) \times S_0^2$$

and expressed as a percentage of MSPE. The entities $\overline{P}$ and $\bar{O}$ are the averaged predicted and observed values, respectively, S_P and S_O are the standard deviations of the predicted and observed values, respectively, and r is the coefficient of correlation between predicted and observed values. The ECT values indicate how the average of predicted values deviates from the average of observed values. The ER values measure deviation of the least squares regression coefficient ($r \times S_O/S_P$) from 1 (the value where the model is completely accurate). A large ER value indicates inadequacies in the ability of the model to predict the variable. The ED value represents the variation in observed values unexplained after the mean and the regression biases have been removed.

Concordance correlation coefficient (CCC), also called reproducibility index, was used to evaluate the precision and accuracy of predicted versus observed values for each model (Lin 1989). The CCC estimate represents as a product of two components. The first component is the correlation coefficient (r) that measures a precision (deviation of observations from the best fit line). Second component is the bias correction factor (C_b) that indicates how far the regression line deviates from the line of unity (accuracy). Another estimate (μ) measures location shift relative to the scale (difference of the means relative to the square root of the product of two standard deviations), where a negative value indicates over-prediction and a positive value indicates under-prediction of observed values by the model.

The prediction biases of the equations developed in this study (one simple, two multiple, and one non-linear models) and the extant models (IPCC 2006; Ellis et al. 2007; Ramin and Huhtanen 2012; Patra 2014b), which predicted methane production with greater accuracy and precision, were further evaluated in the form of residual plots. The residuals (observed −predicted) were plotted against predicted values. The independent variable predicted methane outputs was centered around the mean predicted value before the residuals were regressed on the predicted value as described by St-Pierre (2003), and mean centered bias and biases at the minimum and maximum values were determined as described by St-Pierre (2003).

3 Results

3.1 Description of dataset

A description of the dietary and animal characteristics included in this database such as BW, nutrient and energy intake, feed digestibility, and methane production is provided in Table 2. The concentrations of crude protein (CP) and neutral detergent fiber (NDF) ranged from 24 to 235 (mean values of 117) g/kg and from 192 to 821 (mean values of 567) g/kg DM, which signified that quality of diets varied widely in this database. The mean concentrations of CP and NDF in the diets suggested that low-to-medium quality diets were mainly included in this dataset. Though the roughage proportions in the diets ranged from 0 to 1000 g/kg, mean forage proportion was high (753 g/kg), indicating predominantly forage-based diets were included in the study. These dietary situations are typical in the tropical parts of the world. The wide range of digestibilities of DM, NDF, CP, and ether extract (EE) in this study suggested that digestibilities varied considerably depending upon dietary chemical composition. The methane emissions expressed in terms of MJ/day, g/kg DM intake, and % of GE or digestible energy intake also ranged widely in the dataset.

3.2 Correlations between methane production and animal and dietary variables

With exception of EE intake (P=0.30), methane production expressed as MJ/day was positively (P=0.002 to <0.001) correlated (r=0.44 to 0.83) with BW, FL, and intakes of all of the

Table 2 Descriptive statistics of the variables in the database used to evaluate methane prediction equations in cattle

Item	N	Min	Max	Mean	SD
Body weight (kg)	142	52.8	871	361	161.9
Chemical composition (g/kg DM)					
Organic matter	131	713	957	911	35.9
Crude protein	128	24.0	235	117	46.8
Ether extract	53	6.41	98.0	29.1	22.0
Neutral detergent fiber	117	192	821	567	147.7
Acid detergent fiber	109	109	514	327	102.6
Lignin	95	7.8	115	47.2	21.6
Non-fiber carbohydrate	50	60	508	199	150
Roughage proportion	136	0.0	1000	753	265.8
Intake					
Dry matter intake (kg/day)	142	1.4	19.2	7.7	3.81
GE intake (MJ/day)	142	27.2	353	137	68.7
DE intake (MJ/day)	113	18.4	229	77.5	42.6
ME intake (MJ/day)	113	15.1	187	62.9	34.5
Digestibility (g/kg DM)					
Dry matter	66	333	751	568	92.8
Organic matter	96	367	775	593	84.7
Crude protein	42	450	753	620	73.6
Neutral detergent fiber	53	236	730	533	111
Acid detergent fiber	23	346	658	483	91.0
Ether extract	37	272	877	689	119
Feeding level[a]	113	0.46	3.83	1.54	0.61
Methane production					
Methane (MJ/d)	142	0.90	22.5	7.99	4.70
Methane (MJ/kg DM intake)	142	0.35	1.78	1.04	0.28
Methane (g/kg DM intake)	142	6.3	52.5	19.1	6.09
Methane (g/kg DDM intake)	69	15.4	69.0	35.8	14.7
Methane (% of GE intake)	142	1.96	10.6	5.84	1.63
Methane (% of DE intake)	113	4.40	22.9	10.9	3.72

Min minimum value in the database, *max* maximum value in the database, *SD* standard deviation, *DM* dry matter, *DDM* digestible DM matter, *GE* gross energy, *DE* digestible energy

[a] Feeding level expressed as multiples of maintenance metabolizable energy intake

nutrients with highest correlation observed for DM and GE intake (Table 3). However, methane production expressed as g/kg DM intake or % of GE intake negatively correlated (P=0.02) with EE intake and FL only and tended to positively correlate (P=0.07 to 0.08) with non-fibrous carbohydrate (NFC) only. Concentration of lignin in diets had a negative (P=0.04) relationship, and concentrations of CP and acid detergent fiber (ADF) had a tendency of positive and negative relationship, respectively, with daily methane emission expressed as MJ/day; however, the relationships were poor. In contrast, methane outputs expressed as g/kg DM intake or % of GE intake correlated positively with NDF (P<0.01) and ADF (P=0.02) concentrations negatively correlated with EE

Table 3 Pearson correlation coefficients (*r*) between animal and dietary variables, and methane production in the database

	Methane (MJ/day)		Methane (g/kg DM intake)		Methane (% of GE intake)	
Items	*r*	*P* value	*r*	*P* value	*r*	*P* value
Body weight (kg)	0.65	<0.001	−0.04	0.65	0.11	0.18
Intake						
DM (kg/day)	0.83	<0.001	−0.07	0.41	−0.04	0.60
GE (MJ/day)	0.83	<0.001	−0.07	0.39	−0.06	0.47
ME (MJ/day)	0.81	<0.001	0.05	0.63	0.04	0.68
DE (MJ/day)	0.82	<0.001	0.06	0.54	0.06	0.56
CP (kg/day)	0.74	<0.001	−0.04	0.70	−0.02	0.86
EE (kg/day)	0.15	0.30	−0.34	0.02	−0.34	0.02
NDF (kg/day)	0.68	<0.001	0.03	0.75	0.05	0.63
ADF (kg/day)	0.59	<0.001	0.01	0.92	0.03	0.76
NFC (kg/day)	0.44	0.002	0.27	0.07	0.25	0.08
Lignin (kg/day)	0.45	<0.001	0.08	0.45	0.06	0.60
Feeding level	0.46	<0.001	−0.29	0.002	−0.29	0.002
Nutrient concentration (g/kg DM)						
CP	0.16	0.07	−0.15	0.09	−0.16	0.07
EE	−0.04	0.77	−0.38	0.006	−0.39	0.005
NDF	−0.05	0.56	0.26	0.006	0.25	0.007
ADF	−0.17	0.08	0.22	0.02	0.22	0.02
NFC	−0.01	0.95	0.07	0.64	0.05	0.75
Lignin	−0.22	0.04	0.03	0.77	−0.05	0.64
Roughage proportion (g/kg DM)	−0.09	0.30	0.30	<0.001	0.32	<0.001

DM dry matter, *GE* gross energy, *ME* metabolizable energy, *DE* digestible energy, *CP* crude protein, *EE* ether extract, *NDF* neutral detergent fiber, *ADF* acid detergent fiber, *NFC* non-fibrous carbohydrate

concentration ($P<0.01$) and tended ($P=0.07$ to 0.09) to correlate with CP concentration; however, correlations between methane emission as g/kg DM intake or % of GE intake and concentrations of lignin and NFC were not significant ($P>0.10$). Roughage proportion in the diets correlated ($P<0.001$) positively with methane production when expressed as g/kg DM intake or % of GE intake, but not with daily methane outputs.

3.3 Prediction equations for methane production

Prediction models for enteric methane emission were developed using BW, intakes of DM, nutrients (NDF, ADF, CP, EE, and NFC) and energy (GE, ME and GE), and dietary composition of nutrients (CP, EE, NDF, ADF, lignin, and NFC) as predictors (Table 4). The BW of the animals predicted methane production with $R^2=0.43$. With the exception of EE and CP, intake of all nutrients significantly predicted methane outputs as a single predictor. The predictions of methane output were high for intake of DM ($R^2=0.70$; Fig. 1), GE ($R^2=0.69$), DE ($R^2=0.67$), and ME ($R^2=0.66$), but were low for intakes of NDF ($R^2=0.47$), ADF ($R^2=0.37$), and NFC ($R^2=0.20$). Generally, methane prediction was better at low levels of methane emission (Fig. 1). Among the nutrients evaluated as methane predictors, only fiber (NDF and

Table 4 List of developed statistical models used to predict methane production (MJ/day) from cattle

Equation no.	Equation: methane (MJ/day)
Linear 1	$=1.29_{(\pm0.906)}+0.878_{(\pm0.125)}\times\text{DMI}$; $n=142$, RMSE=5.49; $R^2=0.695$
Linear 2	$=2.752_{(\pm0.705)}+0.0822_{(\pm0.0107)}\times\text{MEI}$; $n=113$, RMSE=5.81; $R^2=0.656$
Linear 3	$=1.480_{(\pm0.892)}+0.0479_{(\pm0.0069)}\times\text{GEI}$; $n=142$, RMSE=5.53; $R^2=0.690$
Linear 4	$=2.787_{(\pm0.943)}+0.0679_{(\pm0.191)}\times\text{DEI}$; $n=113$, RMSE=5.74, $R^2=0.667$
Linear 5	$=-0.077_{(\pm0.933)}+2.584_{(\pm0.483)}\times\text{NDFI}-0.145_{(\pm0.056)}\times\text{NDFI}^2$; $n=117$, RMSE=7.00, $R^2=0.465$
Linear 6	$=0.205_{(\pm0.994)}+4.664_{(\pm0.938)}\times\text{ADFI}-0.529_{(\pm0.197)}\times\text{ADFI}^2$; $n=109$, RMSE=7.86, $R^2=0.365$
Linear 7	$=5.11_{(\pm0.907)}+1.172_{(\pm0.627)}\times\text{NFCI}$; $n=50$, RMSE=7.64, $R^2=0.198$
Linear 8	$=12.26_{(\pm3.035)}-0.0083_{(\pm0.0041)}\times\text{NDF}$; $n=117$, RMSE=9.51, $R^2=0.003$
Linear 9	$=12.54_{(\pm2.925)}-0.0152_{(\pm0.0069)}\times\text{ADF}$; $n=109$, RMSE=9.67, $R^2=0.029$
Linear 10	$=9.81_{(\pm1.111)}-0.0681_{(\pm0.0157)}\times\text{LIG}$; $n=95$, RMSE=9.72, $R^2=0.047$
Linear 11	$=16.82_{(\pm3.629)}-0.0285_{(\pm0.0089)}\times\text{ADF}-0.0275_{(\pm0.0084)}\times\text{NFC}+0.000094_{(\pm0.000033)}\times\text{ADF}\times\text{NFC}$; $n=50$, RMSE=8.20, $R^2=0.117$
Binomial 12	$=-1.012_{(\pm0.709)}+0.308_{(\pm0.249)}\times\text{DMI}+0.0404_{(\pm0.0119)}\times\text{DMI}^2+2.424_{(\pm0.415)}\times\text{NDFI}-0.290_{(\pm0.0409)}\times\text{NDFI}^2$; $n=117$, RMSE=4.94, $R^2=0.738$
Binomial 13	$=-1.490_{(\pm0.745)}+0.418_{(\pm0.232)}\times\text{DMI}+0.0415_{(\pm0.0118)}\times\text{DMI}^2+4.311_{(\pm0.718)}\times\text{ADFI}-0.977_{(\pm0.138)}\times\text{ADFI}^2$; $n=109$, RMSE=4.39, $R^2=0.801$
Linear 14	$=0.157_{(\pm0.712)}+0.102_{(\pm0.0140)}\times\text{BW}^{0.75}$; $n=142$, RMSE=7.51, $R^2=0.429$
Linear 15	$=1.054_{(\pm0.655)}+1.215_{(\pm0.102)}\times\text{DMI}-1.367_{(\pm0.504)}\times\text{FL}$; $n=113$, RMSE=4.57, $R^2=0.785$
Linear 16	$=-1.8503_{(\pm1.570)}+1.255_{(\pm0.146)}\times\text{DMI}-2.529_{(\pm0.685)}\times\text{FL}+0.00857_{(\pm0.00278)}\times\text{GED}$; $n=113$, RMSE=4.47, $R^2=0.796$
Linear 17	$=0.910_{(\pm0.746)}+1.472_{(\pm0.154)}\times\text{DMI}-1.388_{(\pm0.451)}\times\text{FL}-0.669_{(\pm0.338)}\times\text{ADFI}$; $n=91$, RMSE=4.22, $R^2=0.838$
Linear 18	$=-1.559_{(\pm2.010)}+1.217_{(\pm0.164)}\times\text{DMI}-2.418_{(\pm0.724)}\times\text{FL}+0.00714_{(\pm0.00316)}\times\text{OMDm}$; $n=96$, RMSE=4.22, $R^2=0.800$
Monomolecular	$=35.21_{(\pm4.92)}-\{35.21_{(\pm4.92)}+0.250_{(\pm0.157)}\}\times\exp\{-0.0354_{(\pm0.0157)}\times\text{DMI}\}$; $n=142$, RMSE=3.58, $R^2=0.715$
Exponential	$=2.825_{(\pm0.253)}\times\exp\{0.1739_{(\pm0.0111)}\times\text{DMI}\}$; $n=142$, RMSE=5.49, $R^2=0.643$
Mitscherlich	$=71.47_{(\pm22.14)}\times(1-\exp\{-0.0156_{(\pm0.0051)}\times\text{DMI}\}$; $n=142$, RMSE=3.56, $R^2=0.826$
Gompertz	$=1.119_{(\pm0.382)}\times\exp\{(1-\exp(-0.199_{(\pm0.0127)}\times\text{DMI}\times\ln(21.69_{(\pm1.778)}+2\times1.119_{(\pm0.382)})/1.119_{(\pm0.382)}\}-2\times1.119_{(\pm0.382)}$; $n=142$, RMSE=5.72, $R^2=0.661$
Power	$=1.204_{(\pm0.112)}\times\text{DMI}^{0.930(\pm0.0470)}$; $n=142$, RMSE=2.47, $R^2=0.722$

The subscripted data in parentheses are standard error values

BW body weight (kg), *NDF* neutral detergent fiber (g/kg), *ADF* acid detergent fiber (g/kg), *NFC* non-fibrous carbohydrate (g/kg), *DMI* dry matter intake (kg/day), *NDFI* NDF intake (kg/day), *ADFI* ADF intake (kg/day), *NFCI* NFC intake (kg/day), *GEI* gross energy intake (MJ/day), *DEI* digestible energy intake (MJ/day), *MEI* metabolizable energy intake (MJ/day), *FL* feeding level as multiple of maintenance requirement, *OMDm* organic matter digestibility (g/kg) at a maintenance level of feeding (Ramin and Huhtanen 2013), *GED* gross energy digestibility (g/kg), *RMSE* root mean square error

ADF and lignin) concentrations predicted methane emissions, but the prediction were very low ($R^2=0.003$ to 0.05). Even the multiple regression model using nutrients (NDF and ADF as predictors) had low predictive ability ($R^2=0.12$). Methane emission was not predicted by the concentrations of CP, NFC, and EE in this database. Multiple regression models containing intakes of DM and NDF ($R^2=0.74$), DM and ADF ($R^2=0.80$), DM intake and FL ($R^2=0.79$), as two independent variables in the models improved methane prediction compared with a single predictor, and inclusion of each of these variables had a significant effect on the

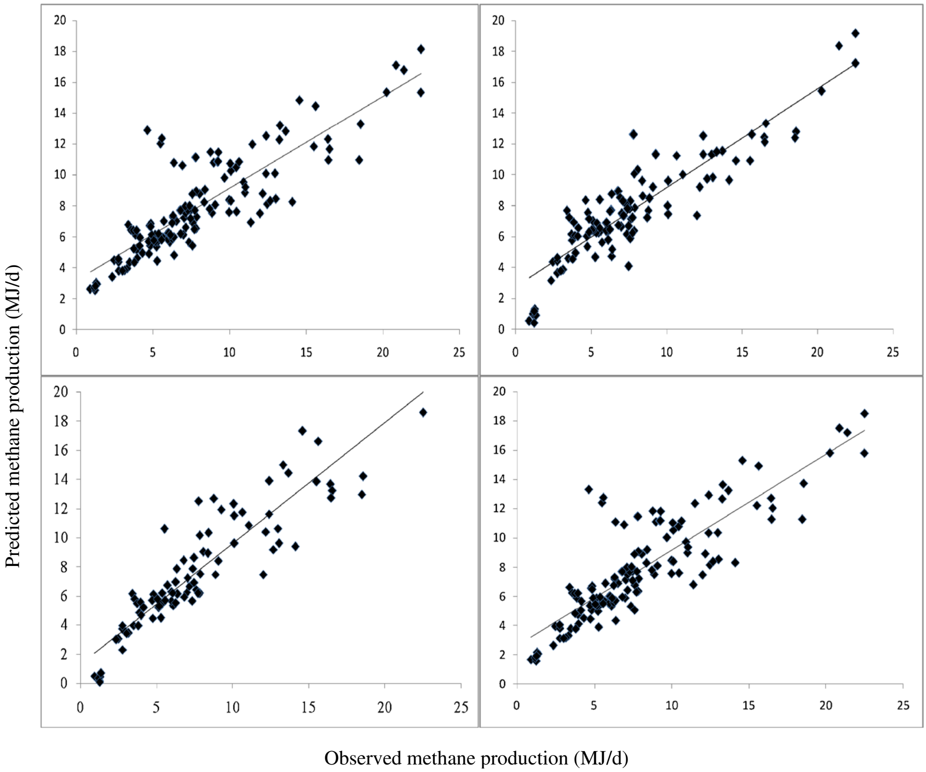

Fig. 1 Predicted versus observed methane production (MJ/day), where methane is predicted by Eq. 1 (*top left*), Eq. 12 (*top right*), Eq. 17 (*bottom left*), and Mitscherlich model (*bottom right*)

relationship. Among the multiple regression equations with three independent variables, the model containing DM intake, ADF intake, and FL improved the model fit to a little extent (R^2=0.84) compared with the models containing DM intake, FL, and OM digestibility (R^2= 0.80), and DM intake, FL, and GE digestibility (R^2=0.80). Any other independent variables and interaction terms in the multiple regression equations did not further improve prediction of methane emission.

Dry matter intake was used to predict methane emission using non-linear models as DM intake had most predictive ability as a single factor of methane prediction. However, exponential growth (R^2=0.64) and Gompertz (R^2=0.66) models did not improve prediction of methane outputs further compared with the linear model using DM intake (R^2=0.70) as a single predictor. Monomolecular (R^2=0.72) and power model (R^2=0.72) marginally and Mitscherlich model (R^2=0.82) greatly improved methane prediction with higher R^2 and lower RMSE values compared with the linear model.

3.4 Comparison of models

Analyses of RMSPE and CCC of the developed methane prediction equations (Table 5) suggested that equation based on DM intake was the best predictor of methane production among the simple models considering smaller RMSPE (31.0 %, of which 92 % due to random error), greater precision (CCC values=0.80), and accuracy (C_b=0.94), followed by GE intake

Table 5 Mean square prediction error analysis using developed and extant methane prediction equations

Study	Equation no.	RMSPE%	ECT%	ER%	ED%	CCC	r	C_b	μ
This study	Linear 1	31.0	0.099	7.71	92.2	0.80	0.85	0.94	0.021
	Linear 2	35.0	1.41	18.5	80.1	0.73	0.84	0.87	0.094
	Linear 3	31.9	0.013	7.21	92.8	0.79	0.84	0.93	0.008
	Linear 4	34.2	0.64	18.3	81.1	0.74	0.85	0.88	0.061
	Linear 5	42.8	0.45	3.20	96.4	0.61	0.71	0.87	0.063
	Linear 6	47.1	0.66	2.43	96.9	0.51	0.63	0.81	0.089
	Linear 7	49.6	0.010	4.48	95.5	0.31	0.52	0.60	0.015
	Linear 8	61.5	0.58	16.9	82.5	0.30	0.62	0.49	0.13
	Linear 9	61.2	0.67	14.1	85.3	0.36	0.63	0.58	0.12
	Linear 10	63.5	10.9	13.5	75.7	0.33	0.63	0.52	0.53
	Linear 11	65.8	36.6	10.5	52.9	0.24	0.63	0.39	−1.20
	Binomial 12	31.4	0.102	12.8	87.1	0.81	0.87	0.93	0.020
	Binomial 13	25.8	0.011	8.18	91.8	0.89	0.91	0.97	0.005
	Linear 14	43.3	1.09	1.11	97.8	0.56	0.66	0.86	−0.11
	Linear 15	25.2	2.05	1.46	96.5	0.89	0.90	0.98	0.068
	Linear 16	25.6	0.024	7.50	92.5	0.88	0.90	0.97	0.010
	Linear 17	22.2	0.10	0.29	99.6	0.92	0.92	0.99	0.013
	Linear 18	26.1	1.23	10.9	87.9	0.87	0.91	0.96	0.058
	Monomolecular	31.0	0.33	4.13	95.5	0.81	0.85	0.95	0.037
	Mitscherlich	30.3	0.38	2.03	97.6	0.82	0.85	0.97	0.037
	Exponential	34.9	2.95	2.80	95.3	0.79	0.80	0.99	0.11
	Gompertz	33.0	5.20	0.24	94.6	0.81	0.68	0.98	0.14
	Power	30.2	0.43	2.30	97.3	0.82	0.85	0.97	0.040
Kriss (1930)	Linear	43.1	48.6	4.02	47.4	0.75	0.85	0.88	−0.53
Axelsson (1949)	Linear	51.8	35.2	0.15	64.7	0.54	0.68	0.79	−0.64
Mills et al. (2003)	Linear 1	67.9	80.1	0.83	19.1	0.47	0.85	0.55	−1.25
	Linear 2	67.2	54.3	1.43	44.2	0.32	0.64	0.51	−1.20
	Exponential	44.1	45.0	12.9	42.1	0.74	0.85	0.88	−0.52
IPCC (2006)	Linear	32.5	7.68	2.86	89.5	0.83	0.84	0.98	−0.16
Ellis et al. (2007)	Linear 1	34.9	8.56	18.6	72.9	0.73	0.85	0.85	−0.24
	Linear 2	39.2	0.75	34.1	65.1	0.69	0.86	0.80	−0.077
Yan et al. (2009)	Linear	51.7	58.4	8.38	33.3	0.70	0.85	0.82	−0.66
Ramin and Huhtanen (2013)	Linear 1	40.7	44.0	0.01	56.0	0.74	0.84	0.87	−0.52
	Linear 2	46.6	30.9	1.13	68.0	0.60	0.74	0.80	−0.56
Ramin and Huhtanen (2012)	Non-linear	38.9	38.6	0.29	61.1	0.76	0.84	0.90	−0.45
Patra (2014b)	Linear	33.7	7.87	14.1	78.0	0.75	0.85	0.88	0.21
	Monomolecular	32.5	6.22	7.72	86.1	0.78	0.85	0.92	0.17

RMSPE% root mean square prediction error (RMSPE) expressed as a percentage of the observed mean, *ECT* error due to bias as a percentage of total RMSPE, *ER* error due to regression as a percentage of total RMSPE, *ED* error due to disturbance as a percentage of total RMSPE, *CCC* concordance correlation coefficient, r correlation coefficient estimate, C_b bias correction factor, μ location shift relative to the scale (difference of the means relative to the product of two standard deviations)

(RMSPE%=31.9 with 92.8 % error from random sources and CCC and C_b values of 0.79 and 0.93, respectively). The equations based on nutrient composition had greater RMSPE along with lower precision and accuracy than the other models. Among the multiple regression equations, models containing intakes of DM and ADF and FL resulted in the lowest RMSPE values (RMSPE%=22.2 %) with random error sources of 99.6 % and greater precision (CCC=0.92) and accuracy (C_b=0.99). Among the non-linear models, Mitscherlich model marginally improved the prediction of methane in terms of RMSPE (30.3 % with 97.6 % from random error and lower regression bias of 2.03 %), precision (CCC=0.82), and accuracy (C_b=0.97) compared with simple linear and non-linear models with a single variable as a predictor. The mean biases (difference between predicted and actual data) were low for all models except for model based on lignin concentration, and concentrations of NDF and ADF. As number of treatments varied among the variables depending upon the available data,

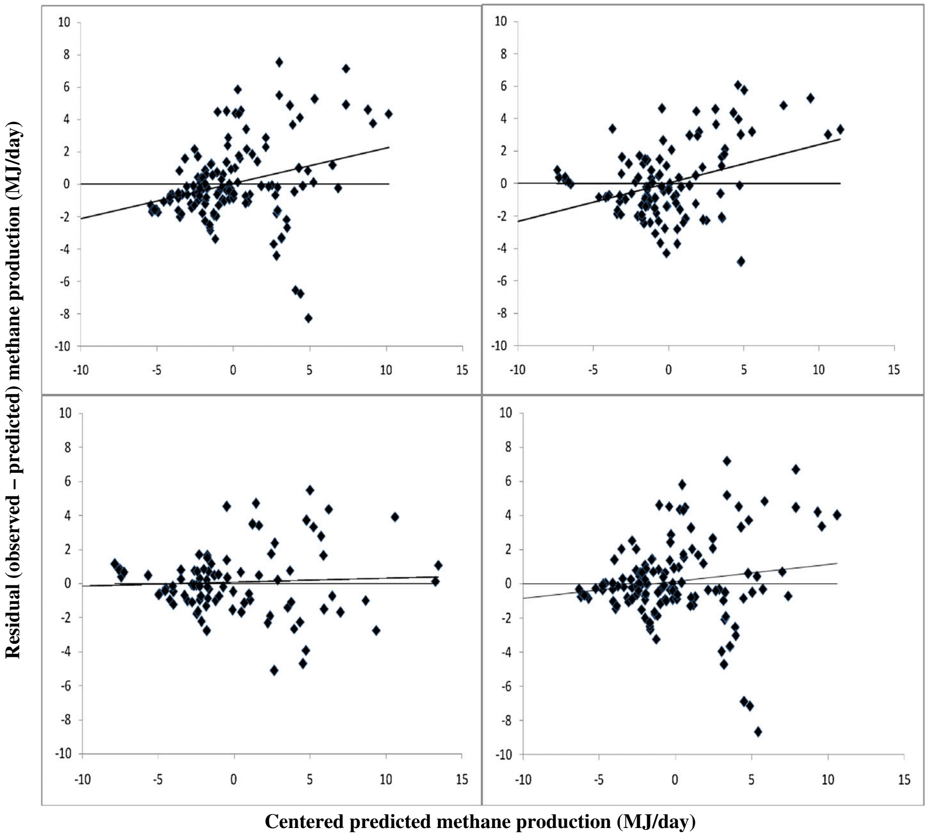

Fig. 2 Plot of observed minus predicted methane production (residual) versus predicted methane production from cattle. The independent variable (predicted methane production) was centered around the mean predicted value before the residuals were regressed on the predicted values, where for Eq. 1, Y=0.079 (±0.21; P=0.70)+ 0.22 (±0.065; P=0.001) (X − 7.97), R^2=0.08, P=0.001 (*top left*); for Eq. 13, Y=0.041 (±0.20; P=0.84)+0.24 (±0.059; P=0.001) (X − 7.80), R^2=0.12, P=0.001 (*top right*); for Eq. 17, Y=0.061 (±0.14; P=0.50)+0.023 (±0.064; P=0.96) (X − 7.97), R^2=0.002, P=0.97 (*bottom left*); for Mitscherlich model, Y=0.151 (±0.21; P= 0.51)+0.098 (±0.059; P=0.11) (X − 7.89), R^2=0.02, P=0.11 (*bottom right*)

precision and accuracy among the models may impose some biases for the comparison of the models.

With the exception of the models of Patra (2014b), methane emissions were over-predicted by all extant models as indicated by higher negative μ values. The extant models generally had greater RMSPE values and larger mean biases. Among the extant models, the mean biases were lower for IPCC (2006), Ellis et al. (2007), and Patra (2014b) models, and the largest mean bias (80 % of RMSPE) was noted for Mills et al. (2003) linear model. The models of IPCC (2006), Patra (2014b), and Ellis et al. (2007) had also better precision (CCC) and accuracy ($C_{b)}$ among the extant models.

There were no significant mean and linear biases ($P>0.05$) for Eq. 17 and Mitscherlich model (Fig. 2). Although the slope biases, but not mean biases, of Eqs. 1 and 13 were significant statistically, they resulted in maximum biases of 2.30 and 2.57 MJ/day over the full range of predicted values, respectively. In contrast, the mean and linear biases (except for Ramin and Huhtanen 2012) of four best extant equations evaluated in this database were significant ($P<0.05$) and resulted in a maximum biases of 2.15, 3.02, 2.30, and 2.72 MJ/day over the full range of predicted values for models of IPCC (2006), Ellis et al. (2007), Ramin and Huhtanen (2012), and Patra (2014b), respectively (Fig. 3).

4 Discussion

The purpose of this study was to develop statistical models of enteric methane production in cattle of tropical feeding systems and to assess the dietary composition affecting methane production. Majority of the dietary treatment means included in the database were from India ($n=54$) and Brazil ($n=55$). It is imperative to state that major proportion of cattle populations is centered in these countries, and cattle populations are growing in these regions. A sizeable proportion of cattle population is also located in African countries, and cattle population in Africa is expected to grow faster in coming decades (Gerber et al. 2013). However, the literature on in vivo methane production in cattle in Africa is scanty. Thus, the models developed in this study may be less suited to predict methane production and understand feeding strategies in African countries.

The average methane production from cattle of tropical climate was 1.04 MJ/kg DM intake or 5.84 % of GE intake in this study. The methane emission ranged from 1.12 to 1.49 MJ/kg DM (Ellis et al. 2007; Yan et al. 2009) or 6.37 to 10.1 % of GE intake (Wilkerson et al. 1995; Yan et al. 2009) reported for dairy and beef cattle from temperate situations. It appears that methane production per unit of feed intake is lower for tropical cattle production systems than temperate cattle production systems, which is likely due to the lower quality diets (containing low concentration of CP and high concentration of NDF) fed to the cattle in the tropics compared with the diets offered to cattle in temperate countries (Van Soest 1994). Methane is produced during fermentation of feeds in the rumen production. Digestibility of forages and crop residues in tropical countries is low (Van Soest 1994), and consequently, low quality feeds in tropical countries may result in lower methane production per unit of feed intake. For example, Kurihara et al. (1999) studied two tropical grasses, i.e., mature Angleton grass (*Dicanthium aristatum*) hay with NDF digestibility of 55 % and immature Rhodes grass (*Chloris gayana*) hay with NDF digestibility of 69 % for methane production in tropical breed of cattle. Methane production in cattle fed on Angleton grass was lower than in cattle fed on

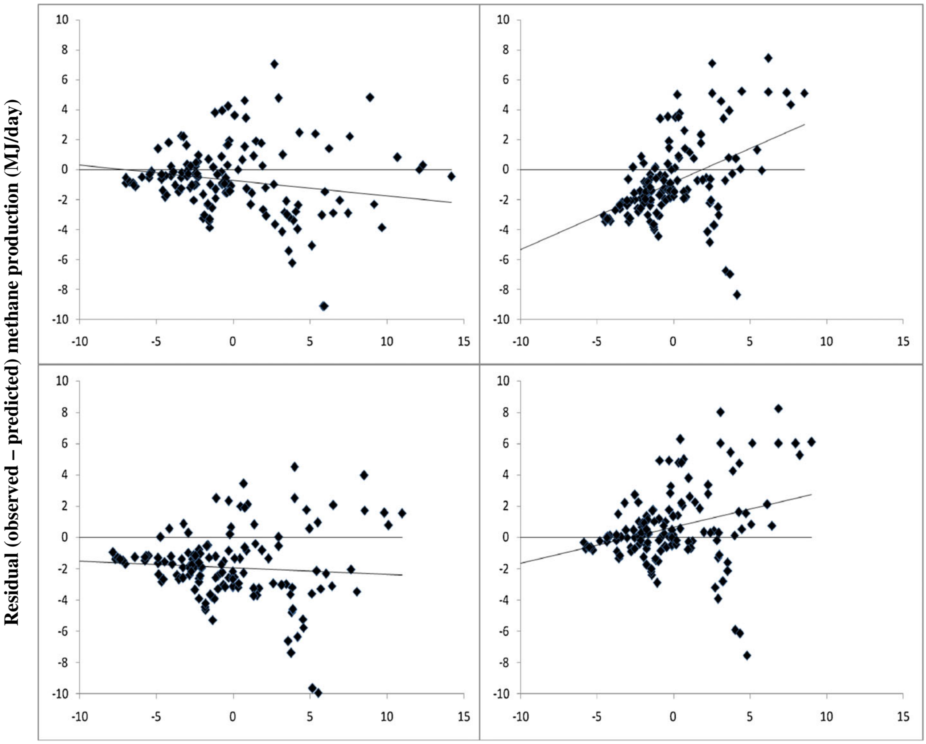

Fig. 3 Plot of observed minus predicted methane production (residual) versus predicted methane production from cattle. The independent variable (predicted methane production) was centered around the mean predicted value before the residuals were regressed on the predicted values, where for equation of IPCC (2006), $Y=-0.73$ (±0.22; $P=0.001$) − 0.10 (±0.050; $P=0.04$) (X − 8.77), $R^2=0.03$, $P=0.04$ (*top left*); for linear equation 1 of Ellis et al. (2007), $Y=-0.82$ (±0.21; $P<0.001$)+0.45 (±0.077; $P<0.001$) (X − 8.87), $R^2=0.20$, $P<0.001$ (*top right*); for linear equation 1 of Ramin and Huhtanen (2012), $Y=-1.95$ (±0.21; $P<0.001$) − 0.042 (±0.052; $P=0.42$) (X − 10.0), $R^2=0.005$; $P=0.42$ (*bottom left*); for equation of Patra (2014b), $Y=0.65$ (±0.21; $P=0.002$)+0.23 (±0.066; $P=0.001$) (X − 7.39), $R^2=0.08$, $P=0.001$ (*bottom right*)

Rhodes grass hay (113 versus 257 g/day and 31.6 versus 36.3 g/kg DM, respectively; Kurihara et al. 1999).

Various models developed in this study clearly demonstrated that intakes of nutrients particularly DM or GE were the stronger determinant of methane production than nutrient composition. There was a strong relationship between methane production and intake of DM or GE. The prediction of methane production was better at low levels of methane production suggesting that other physiological and microbiological factors such as rumen volume and fermentation characteristics in addition to intakes of nutrients may interplay in methane production in the rumen at high level of methane production (Hegarty 2004). A number of studies also reported that feed intake (DM or energy) was a principal determinant for prediction equations of methane emissions in dairy and beef cattle (e.g., Mills et al. 2003; Ramin and Huhtanen 2013; Yan et al. 2009). In this study, R^2 values of 0.69 to 0.70 in the relationship between methane and DM or GE intake were moderately high. Moderate R^2 values of 0.68 with DM intake or 0.70 with GE intake were reported in UK feeding conditions (Yan et al. 2009). However, the prediction equations using DM intake or ME intake as primary predictors of methane outputs had low R^2 values (0.44 or 0.36) in the study with beef cattle (Ellis et al. 2007). Yan et al. (2000) even reported a R^2 value of 0.85 for the methane prediction equation based on GE intake. These differences among the studies may result from the wider variations of the ingredient and chemical composition of diets and animal characteristics in each database. The ME intake and DE intake are expected to be better determinants of methane outputs than DM intake as the former account for methane production within its derivation (Mills et al. 2003). In the study of Mills et al. (2003), ME intake and DE intake were better predictors of methane production than DM intake and GE intake. However, ME and DE intake predicted methane outputs with less precision compared with DM intake in this study. This may be attributed to the inclusion of calculated ME and DE intake values for many studies included in this dataset instead of direct measured values, thus imposing more errors in ME and DE intake values. This result suggests for better characterization of feeds of tropical regions of the countries instead of using calculated nutritive values of feeds. Thus, extensive research activities are needed to characterize tropical feeds for methane production in the context of food security, mitigation of methane production, and climate change adaptation in tropical developing countries. Ellis et al. (2007) also noted a lower precision and accuracy in the prediction of methane production using ME intake than DM intake in dairy (R^2=0.64 versus 0.53) and beef cattle (R^2=0.44 versus 0.36) datasets.

It is imperative that the quadratic term of intakes of DM, GE, DE, or ME as a single determinant was not significant (P>0.05) in predicting methane emission in this study. However, Ramin and Huhtanen (2013) found that the quadratic model containing DM intake as a single predictor improved the goodness of fit compared with the linear model. In contrast, the quadratic term of NDF intake or ADF intake as a single methane predictor in this study, which was negatively related, was significant (P< 0.05). This is expected because particulate passage rate increases to a greater extent with increasing fiber intake compared with other nutrients resulting in lower fermentation of feeds in the rumen and consequently lower methane production. However, many models developed earlier based on fiber intake did not include quadratic term of the fiber fractions (e.g., Mills et al. 2003; Ellis et al. 2007, 2009).

Intake of DM or GE is a key factor in most of the enteric methane emission prediction equation, but is difficult to accurately determine on farms, particularly in grazing conditions. Thus, chemical composition of diets and BW of animals were used for development of prediction equations, as these equations may be useful in situations where intake data may not be available. The BW of animals resulted in a reasonable degree of prediction of methane production. However, concentrations of NDF, ADF, and lignin as a single determinant had lower predictability (R^2=0.003 to 0.05) of methane outputs in the database, and goodness of fit of these equations was very low. Even the multiple regression equation based on dietary composition had low predictability (R^2=0.12). However, nutrient composition of diets predicted methane outputs with relatively high R^2 values in the studies of Mills et al. (2003) (R^2=0.24 to 0.35) and Ellis et al. (2007) (R^2=0.01 to 0.35). The low relationship between nutrient composition and methane production in this study is likely due to greater variations of dietary nutrient composition and nutritive values in tropical climates compared with the temperate climates (Van Soest 1994). Tropical feeds have also low predictability of nutritive values from fiber components (Van Soest 1994). Dietary EE was negatively correlated with methane production, and the prediction model for methane production included EE as a predictor when the database included the studies with dietary fat supplementation (e.g., Grainger and Beauchemin 2011; Moate et al. 2011; Patra 2013). However, EE in this study was not associated with methane production, which was presumably due to the presence of low concentrations of EE (29±22 g/kg DM) in the diets. Ellis et al. (2007) reported that the multiple regression equation containing DM intake and EE intake improved the prediction of methane production in the beef database, but not in the dairy database.

Multiple regression equations were presented when they improved the prediction compared with simple regression equations. In simple regression equations, the quadratic term was not significant for DM, but the multiple regression equations contained significant positive quadratic effect of DM and negative quadratic effect of NDF or ADF. This might suggest that methane production is influenced by DM intake as well as fiber intake. The FL was negatively related in the multiple regression equations, suggesting that FL influences methane production mediated probably through changes in passage rate and rumen digestion of feeds (Ramin and Huhtanen 2013). The most improved multiple regression equations developed by Ellis et al. (2007) included ME intake, ADF intake, and lignin intake as determinants with R^2= 0.85 for the beef dataset, and DM intake, NDF intake, and lignin intake with R^2=0.71 for the combined beef and dairy dataset. In the present database, lignin had no significant contribution in the prediction of methane in any multiple regression models.

Methane production in the rumen depends upon dietary factors, rumen functions, and fermentation dynamics and may not follow a linear trend over a wide range of values. Therefore, nonlinear regression models were also evaluated for prediction of methane emission using DM intake. Among the non-linear models, Mitscherlich model improved the relationship between methane production and DM intake compared with the simple linear models. Although Mills et al. (2003) noted that there was a minor difference in RMSPE percentage between the linear and non-linear models for the UK data, the benefits were evident for the American and Northern Ireland data for lactating cows. It is evident that the non-linear models of Ramin and Huhtanen (2012) and Mills et al. (2003) performed slightly better than the linear models of Ramin and Huhtanen (2013) and Mills et al. (2003) when they were challenged with this database. Thus, the non-linear models may be better for predicting methane production in a wide range of intake and dietary variables, which has also been suggested by Mills et al. (2003). Nonetheless, the prediction of methane production should be made with caution when dependent variables are outside the range of this database because few models have intercept values that are not biologically relevant.

Several extant regression equations were used to validate the predictability of methane production in this database. The newly developed models generally performed better than the extant models as these equations had lower RMSPE values compared with the extant models. Among the extant models, the equations of IPCC (2006) and Patra (2014b) had better goodness of fit in this database. This is because IPCC (2006) considered both tropical and temperate feeding situations; Patra (2014b) included most of the data from tropical countries of buffalo production system. The lower accuracy and precision of the extant models developed from cattle of North America and European situations compared with new equations developed in this study may be attributed to the animal type, geographical and dietary differences (King et al. 2011; Wright and Klieve 2011). Among extant equations, few simple DM intake models were quite good compared with multiple regression models developed in this study (e.g., Ellis et al. 2007; Ramin and Huhtanen 2013) when challenged in this database. This indicates that the parameters in those models derived using temperate cattle are unable to reflect the associations in tropical cattle. The diets in this study were of low to medium quality whereas the diets for cattle in North America and European countries were of medium to high quality. Besides, the breeds of the tropical countries are mainly of zebu types, which have low nutrient requirements due to low body weight and productivity. Preparation of inventory of methane emissions as per methodology of IPCC (2006) tier II requires country-specific methane conversion factors (Ym; methane production as a proportion of GE intake) for each categories of livestock, but many tropical countries, especially in Africa and Asia, do not have country-specific Ym because of lack of information of the methane energy loss as a percentage of GE intake for those countries. The enteric methane production based on the activity data of Patra (2012) and IPCC (2006) tier II methodologies, methane production from Indian cattle was 7736 Gg/year in 2007. However, methane production from Indian cattle using the same activity data and model 1 and model 3 was 5665 and 5703 Gg/year, respectively, in 2007, which was considerably (26.5 %) lower compared with the estimates based on the IPCC (2006) methane conversion factor. The models reported in this study should be considered for more accurately preparing the enteric methane emission inventories for cattle in the tropical countries.

5 Conclusions

Linear models developed based on DM intake or GE intake as a single predictor improved the prediction of methane production. The multiple regression equation based on intakes of NDF, ADF, and NFC improved the goodness of model fit and had better precision and accuracy than the linear models. Among the nonlinear models, Mitscherlich model performed better than simple linear models. The extant models developed for cattle in temperate production systems over-predicted methane emissions, when they were challenged in this database, and most of these extant equations except IPCC (2006) had low precision and accuracy for the prediction of methane outputs from cattle of tropical feeding situations. A better estimate of enteric methane emissions by livestock species using IPCC (2006) tier II and III methodologies requires different activity data such as animal numbers in different categories and ages of each animal species, milk production, growth rate, dietary composition, feed availability, energy/DM requirements, and country-specific Ym and methane emission (i.e., per animal annually) factors. The IPCC (2006) developed methodologies to estimate enteric methane emissions with the use of Ym. However, Ym does not directly represent variations in methane emissions determined by the ruminal fermentation of distinct carbohydrates and feeding levels. Thus, the usefulness of Ym based models in predicting enteric methane emissions and evaluating dietary methane mitigation options is limited (Moraes et al. 2014). Furthermore, the low predictive ability of the Ym approach may introduce considerable inaccuracy in preparation of enteric methane emission inventory (Ellis et al. 2010; Patra 2014b). The equations developed in this study will be valuable to estimate country-specific Ym and methane emission factors using feed intake and diet characteristics, which will be useful for more accurately preparing enteric methane emission inventory data from cattle in tropical regions of the countries instead of using default enteric methane emissions factors of IPCC (2006) when other activity data are available. Moreover, this study specifies a better understanding of dietary factors influencing methane production in cattle for tropical production systems. Nonetheless, these newly developed models should be evaluated on an external database for testing the goodness of fit of the prediction equations of methane production from cattle in the tropics.

Compliance with ethical standards

Conflicts of interest Author declares that there is no conflict of interest.

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