Prediction of enteric methane production in beef cattle

by

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ABSTRACT

Methane (**CH_4**) is a greenhouse gas with an elevated global warming potential (**GWP**) equivalent to 28 times that of CO_2. Also, production of enteric CH_4 results in a 2 to 12% loss of the gross energy intake of cattle thus knowing the amount of CH_4 released to the environment is important. The overall objective of this research was to evaluate the accuracy and precision of predicted values of enteric CH_4 production from models compared with observed values. The first study used concordance correlation coefficient (**r_c**), root mean square prediction error (**RMSPE**, g d^{-1}), model efficiency, and analysis of errors to assess precision and accuracy of fifty-one published empirical models that predict CH_4 production. An original database comprised of 221 treatment means of CH_4 production from 53 in vivo beef studies divided into high- and low- forage datasets was used to evaluate the predictions. Using a combined index of statistics, the best-fit models for the high-forage dataset were ranked in decreasing order: Intergovernmental Panel on Climate Change (**IPCC**) Tier 2 method (IPCC 2006), 3 models from Moraes et al. (2014; steers animal level, simulated gross energy (**GE**) at the animal level, steers GE level), and equation N from Ellis et al. (2009). For the high-grain diets, the best-fit models were: equation I Ellis et al. (2009), equation GEI from Ricci et al. (2013), and equations for steers at the GE level, animal level and simulated GE level from Moraes et al. (2014). Two conclusions emerge from this study: 1) Ranking of models differs with forage content of the diet and, 2) Extant models are generally imprecise and lack accuracy, especially when used for low- forage diets. The second study was conducted to develop universally

applicable empirical models that predict CH_4 specifically for high- and low- forage diets using traditional and resampled databases to obtain new models. The best fit models for high- and low- forage diets were obtained from Monte Carlo datasets and included the following variables: body weight (kg) and intakes (kg d^{-1}) of dry matter, fat, neutral detergent fiber (**NDF**), acid detergent fiber (**ADF**), crude protein:NDF and starch:NDF ratios. For high- and low forages, best-fit models had $r_c \geq 0.70$ and RMSPE ≤ 40 g CH_4 d^{-1}, $r_c \geq 0.90$ and RMSPE ≤ 15 g eCH_4 d^{-1}, respectively. In this study it was concluded that the uncertainty of estimating beef cattle enteric CH_4 emission compared with the IPCC Tier 2 methodology is reduced when using models specific to dietary forage proportion. The third study was conducted to estimate the variability of CH_4 emissions using sixteen different models including the newly developed models and monthly simulated diets for mature beef cows and growing beef cattle in Eastern and Western Canada. Predictions were compared to those using an IPCC (2006) Tier 2 approach. Results indicated that there was variability in predicted CH_4 production and conversion factor (**Ym**, percentage of gross energy intake) among models. Models that use variables that indirectly contain other variables such as dry matter intake (**DMI**) or energy predict stable Ym values and generate results similar to those using IPCC (2006). However, these models are less sensitive to changes in diet composition. In contrast, variability in Ym predictions was greater for models that consider diet composition.

Using high- and low-forage datasets that were globally represented, it was found that extant beef cattle enteric CH_4 models lack accuracy. Due to the lack of accurate models, the 2nd study developed new models that improved the prediction of

CH_4 production from beef cattle. Using a simulated production system for mature beef cows and growing steers in Canada the final study revealed variability of CH_4 predictions between IPCC 2006 Tier 2 and models that account for nutrient intakes of cattle consuming high- or low-forage diets. The results of this research enable beef farm advisers, researchers and government policy advisors to choose appropriate equations to estimate enteric CH_4 emissions from beef cattle under various dietary conditions. Accurate prediction of enteric CH_4 emission is critical for the beef industry to develop suitable policies and adopt feeding strategies to decrease the quantity of enteric CH_4 released to the atmosphere.

PREFACE

This thesis is an original work by Carlos Paul Escobar-Bahamondes. The research project, of which this thesis is a part, was supported by Agriculture and Agri-Food Canada.

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DEDICATION

To Jimena, Consuelo, Daniel and Cristobal little giants in middle of my journey, without your looks, answers, laughs, worries, complaints, understanding and love …… I am nothing.

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At the end of this journey, this work and my academic achievements are the result of a chain of unique events. In this chain there are a lot of people who contributed in different ways to my life in Canada, my work, my achievements and this document.

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[H]	Metabolic hydrogen
ADF	Acid detergent fibre
ADG	Average daily gain
ADL	Acid detergent lignin
AL	Animal level
ATP	Adenosine triphosphate
BW	Body weight
CD	Coefficient of model determination
CI	Combined index
CEL	Cellulose
CF	Crude fiber
CH_4	Enteric methane
CO_2	Carbon dioxide
CO_2-eq	CO_2-equivalent
CP	Crude protein
CV	Coefficient of variation
DE	Digestible energy
DL	Dietary level
DM	Dry matter
DMD	Dry matter digestibility

DMI	Dry matter intake
dr	Index of agreement
ECT	Error due to overall bias
ED	Error due to the disturbance (random error)
EE	Ether extract
ER	Error due to deviation of the regression slope from unity
FA	Fatty acids
F:C	Forage:concentrate ratio
GE	Gross energy
GEI	Gross energy intake
GEL	Gross energy level
GHG	Greenhouse gas
Gt	Gigaton (1Gt = 100,000,000 metric tons)
GWP	Global warming potential
H_2	Hydrogen gas
H	Heifers
HC	Hemicellulose
HF	High-forage
IA	Index of agreement
IPCC	Intergovernmental Panel on Climate Change
LCA	Life cycle assessment
LF	Low-forage
MAE	Mean absolute error

MC	Monte Carlo
ME	Metabolizable energy
MEF	Model efficiency
MEI	Metabolizable energy intake
MJ	Megajoules
mo	Months
Mt	Metric tons
MSPE	Mean square prediction error
N_2O	Nitrous oxide
NADH/NAD+	Nicotinamide adenine dinucleotide
NASEM	National Academies of Sciences, Engineering, and Medicine
NDF	Neutral detergent fibre
NFC	non-fiber carbohydrate
NFE	Nitrogen free-extract
NSC	Non-structural carbohydrates
OM	Organic matter
OMD	Organic matter disappearance
PCA	Principal component analysis
ppb	Parts per billion
r_c	Concordance correlation coefficient
RMSPE	Root mean square prediction error
S	Steers
SD	Standard deviation

SF_6	Sulfur hexafluoride tracer gas technique
SIM	Values calculated or simulated
Tg	Teragram (1 Tg = 1,000,000 metric tons)
VFA	Volatile fatty acids
Ym	Conversion factor rate (% of GEI)

CHAPTER 1. Literature review

1.1. Introduction

The interest in methane (**CH_4**) started in the 18th century when Italian physicist Alessandro Volta (1745-1827) identified this gas in the bubbles that rose from a swamp as being flammable (Reay et al. 2010). Joseph Fourier (1768-1830) estimated that an object the size of the Earth receiving radiation from the Sun should be colder than the planet actually was; concluding that the Earth's atmosphere might act as an insulator. Years later, John Tyndall (1820-1893) evaluated absorptive properties of gases, and discovered that gases have different capacities to absorb infrared radiation, proving that atmospheric gases have greenhouse effects (Reay et al. 2010), meaning that like in a glass house, gases act as a semi-permeable barrier that let heat into the atmosphere but prevent its escape to exterior space.

Methane is a tetrahedral molecule with four C-H bonds, and belongs to the organic group called alkanes. In the natural state it is found below ground, under the sea floor and in the atmosphere. Methane can be produced in different ways: (1) methanogenesis, which is a form of anaerobic respiration to obtain energy used by microorganisms present in landfills, ruminants and the gut of termites, (2) "power to gas", a process that converts electricity power to a gas using the pathway carbon dioxide (**CO_2**) + H_2O -> CH_4, (3) industrial processes, (4) synthesis in the laboratory, and (5) serpentinization, a process whereby a rock is changed with the addition of water into the crystal structure of the minerals found within the rock. Methane is a colorless and odorless gas at room temperature and standard pressure ([Online] Available: http://en.wikipedia.org/wiki/Methane - Production [2016 May. 07]).

1.2. Methane in the atmosphere

In 2011, atmospheric concentrations of the greenhouse gases (**GHG**) CO_2, CH_4, and nitrous oxide (**N_2O**) were 391 ppm, 1,803 parts per billion (**ppb**), and 324 ppb, respectively. These concentrations are unprecedented in the last 22,000 years and exceed the highest concentrations recorded in ice cores during the past 800,000 years (Intergovernmental Panel on Climate Change (**IPCC**) 2013). In pre-industrial times, concentrations of CH_4 in the atmosphere were closer to 722 ppb, thus there has been a large increase in concentration to today's levels (Ciais et al. 2013; Figure 1.1).

Methane concentration is higher in the Northern Hemisphere than in the Southern Hemisphere because of greater ruminant populations, activities associated with production and use of fossil fuels, expansion of rice crops, more land than the Southern Hemisphere and emissions from landfills in the Northern Hemisphere (IPCC 2013; Figure 1.2).

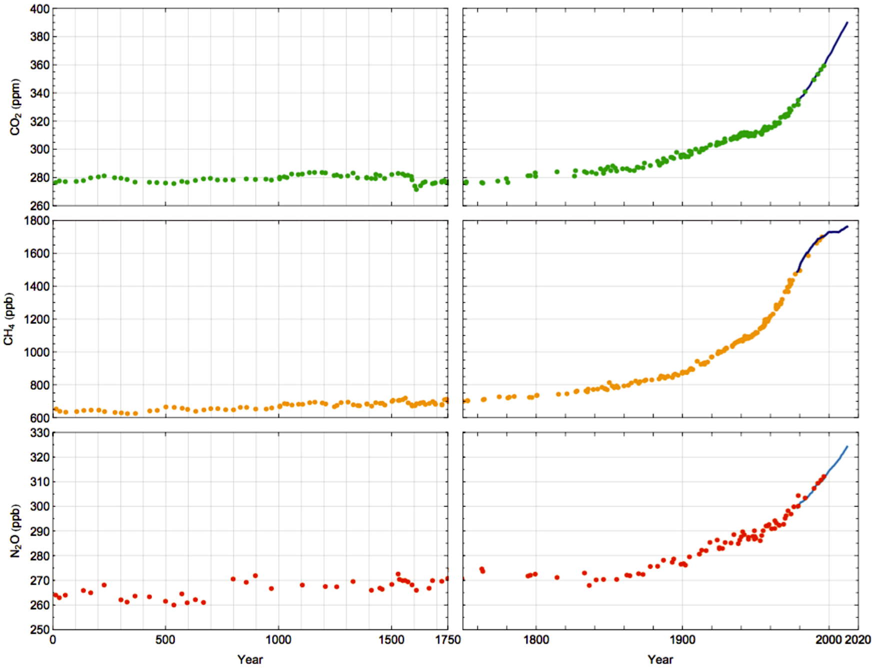

Figure 1.1. Changes in atmospheric CO_2, CH_4, and N_2O concentrations over the industrial era (1750-2020) and pre-industrial era (0-1750) (From IPCC 2013).

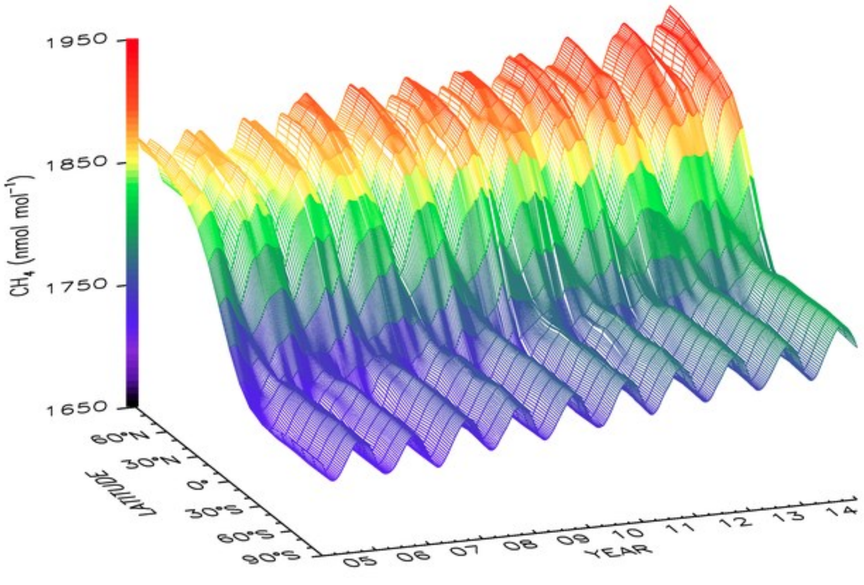

Figure 1.2. Global distribution of atmospheric methane (From NOAA/ESRL ([Online] Available: http://www.esrl.noaa.gov/gmd/ccgg/figures/ [2016 Jun. 01])

The global CH_4 project ([Online] Available: http://www.globalcarbonproject.org/methanebudget/13/hl-compact.htm [2016 May. 06]) estimated for the decade 2000-2009, global emissions of CH_4 from natural and anthropogenic causes were 548 Teragram (**Tg**; 1 Tg = 1,000,000 metric tons) CH_4 per year with a global sink estimated at 540 Tg CH_4 per year, resulting in net emissions of +8 Tg CH_4 per year. Emissions from anthropogenic CH_4 sources ranged between 50% and 65% of the global emissions in the 2000s. These sources include rice paddies, ruminants, waste, landfills, and fossil fuel extraction and associated activities (Ciais et al. 2013). Total emissions from human activities for the decade 2000-2009 were computed to be an average of 331 Tg CH_4 per year with the most important sources being fossil fuels (26-32%), ruminants (26-28%), and landfills/waste (20-27%) ([Online] Available: http://www.globalcarbonproject.org/methanebudget/13/hl-compact.htm [2016 May. 06])

Methane is one of the most recognized GHG and there is no doubt that the livestock sector represents a significant source of anthropogenic CH_4 because of ruminal fermentation (Hristov et al. 2013). Global Warming Potential (**GWP**) is defined by IPCC as an indicator of the relative effect of a GHG in terms of climate change considering a fixed time period, such as 100 years, compared with the same mass of CO_2 (Gerber et al. 2013a). Methane has a GWP equivalent to 28 times that of CO_2 calculated over a 100-year timeframe or 84 times that of CO_2 if the timeframe is 20 years (IPCC 2013). However, in successive reports from IPCC, which only considers the timeframe over 100 years, the GWP of CH_4 value has changed slightly due to a change in the estimated lifetime of CH_4 in the atmosphere. Thus, the GWP value was 23 in 2001, 25 in 2007, and 28 in 2013 (IPCC 2001; IPCC 2007; IPCC 2013, respectively).

1.3. Global emissions of GHG from the beef cattle sector

Livestock contributes to climate change by emitting GHG in the form of CH_4 released from ruminal fermentation and CH_4 and N_2O from feces or indirectly by emissions from feed production, conversion of forest to pasture and transportation.

Carbon dioxide equivalent (**CO_2-eq**) is the amount of CO_2 emissions that would cause the same time-integrated radiative force, over a given time period, as an emitted amount of a mixture of GHGs. It is obtained by multiplying the emission of a GHG by its GWP for a given time period (Gerber et al. 2013a).

Total GHG emissions from the global livestock sector have been estimated at 7.1 Gt CO_2-eq per year, representing 14.5% of total emissions from anthropogenic sources (Gerber et al. 2013a). The main sources of GHG from livestock systems are CH_4 (43%) from enteric fermentation from ruminants, N_2O (29%) from manure and CO_2 (27%) from land use change (Gerber et al. 2013a). Beef and dairy production contributes 41 and 20% of global livestock emissions, while pig meat and poultry (meat and eggs) production contributes 9 and 8%, and other classes (e.g., buffalo, sheep, goats) contribute 22% (Gerber et al. 2013a). According to Gerber et al. (2013), beef cattle emit 2,495 million tonnes of CO_2-eq mostly as enteric CH_4 (77%). Using a GWP of 25 (IPCC 2006) the production of CH_4 from beef cattle is equivalent to 68.61 Tg per year with 2005 as the reference year. Thus, beef cattle are the largest source of CO_2-eq emissions to the environment within the global livestock sector (Herrero et al. 2011; Gerber et al. 2013a).

1.3.1. National GHG emissions in Canada

The United Nations Framework Convention on Climate Change (**UNFCCC**) is an international environmental agreement established at the "Rio Earth Summit" in Rio de Janeiro in June 1992 to cooperatively address climate change issues. The objective of the UNFCCC is: "*stabilization of GHG concentrations in the atmosphere at a level that would prevent dangerous anthropogenic interference with the climate system*". ([Online] Available: http://unfccc.int/essential_background/background_publications_htmlpdf/application/pdf/conveng.pdf [2016 May. 09]). In December 2015, Canada and 194 other countries pledged to sign the Paris agreement to fight against climate change. The stated goal is: "*to limit the global average temperature rise to well below 2 degrees Celsius above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5 Celsius degrees above pre-industrial levels, recognizing that this would significantly reduce the risks and impacts of climate change*" ([Online] Available: http://unfccc.int/resource/docs/2015/cop21/eng/l09r01.pdf [2016 May. 09])

Canada developed its environment policy with a commitment of reducing its GHG emissions by 17% below the 2005 level by the year 2020 and intending to reduce GHG emissions by 30% below 2005 levels by 2030 (Environment and Climate Change Canada 2016).

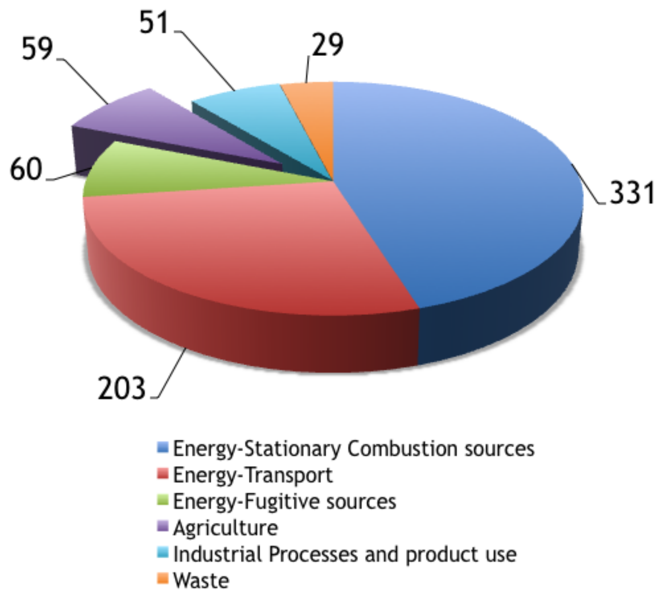

Figure 1.3. Canada emissions (Mt CO_2-eq) in 2014 by IPCC sector (From Environment and Climate Change Canada, 2016)

In 2014 the total emissions in Canada were estimated as 733 Mt CO_2-eq excluding estimates from land use and land-use change and forestry (Figure 1.3). The Energy sector accounted for the majority of Canada's total GHG emissions in 2014, equivalent to 81% (594 Mt CO_2-eq) of total emissions, followed by the agriculture sector that contributed 8% (59 Mt CO_2-eq). The enteric fermentation (42.3%, 25 Mt CO_2-eq) is the principal agricultural emission followed by agricultural soils (39.0%, 23 Mt CO_2-eq), manure management (13.6%, 8 Mt CO_2-eq) and application of lime, urea and other fertilizers that contain carbon (5.1%, 3 Mt CO_2-eq) (Environment and Climate Change Canada 2016).

1.3.2. Canada’s CH_4 emissions from the beef cattle sector

According to statistics released by the Food and Agricultural Organization (**FAO**), the world had 1,482,144,415 head of cattle of which 12,220,000 cattle (0.82%) were in Canada in 2014. For Canada, in 2013, cattle represented an export value of US$ 1,323,358,000, which is about 15% of the total world export value. In contrast, enteric fermentation expressed as Tg CO_2-eq in Canada contributes only 1.0% (≈15.10 Tg) of total world emissions for cattle (1,522.3 Tg CO_2-eq) or one-seventh of what the USA emits (112.7 Tg CO_2-eq from enteric fermentation) ([Online] Available: http://faostat3.fao.org [2016 Jul. 05]).

In 2014, the Canada beef industry had 10.2 million head of beef cattle (Table 1.1), which accounted for about 20 Mt CO_2-eq from enteric fermentation representing 33.8% of total emissions CO_2-eq from Canadian agriculture. Emissions from the beef industry peaked in 2005 with 26 Mt CO_2-eq, and decreased to 20 Mt CO_2-eq in 2014, due to a reduction in the beef cattle population, which stabilized in 2011. In 2015, CH_4 emissions from beef cattle represented 80.0% of the total CH_4 emitted by livestock in Canada (Environment and Climate Change Canada 2016).

Table 1.1. Greenhouse gas emissions from agriculture and the beef cattle sector (Adapted from Cansim 2016 and Environment and Climate Change Canada 2016)

	2000	2005	2010	2011	2012	2013	2014
Beef cattle (Million)	10.9	12.7	10.7	10.2	10.2	10.3	10.2
	GHG emissions (kt CO_2-eq)						
Agriculture total	59,000	61,000	57,000	56,000	58,000	60,000	59,000
[a]Enteric CH_4	28,000	31,000	26,000	25,000	25,000	25,000	25,000
Beef cattle enteric CH_4	23,000	26,000	21,000	20,000	20,000	20,000	20,000
Beef cattle enteric CH_4 / Agriculture total GHG	39.0%	42.6%	36.8%	35.7%	34.5%	33.3%	33.9%
Beef cattle enteric CH_4 / Enteric CH_4	82.1%	83.8%	80.7%	80.0%	80.0%	80.0%	80.0%

Note: [a] Total Livestock.

Under the terms of the 1997 Kyoto protocol, signatory nations are required to submit an annual national inventory of GHG emissions (Garnsworthy et al. 2012). Normally, GHG and particularly CH_4 inventories are calculated using methodologies suggested by the IPCC 2006. These methodologies are classified as Tier 1, 2 and 3, which relate to the expected level of accuracy of that estimate and level of availability of data within a particular country. To estimate the national inventory using the Tier 1 approach, the number of animals according to species and subgroup is multiplied by an emission factor. For beef cows in North America, Tier 1 methodology suggests 53 kg CH_4 yr^{-1} as a fixed emission factor per head. Tier 2 methodology uses a CH_4 conversion factor (**Ym**) of 6.5 ± 1% of gross energy intake for dairy cows and beef cattle that are fed forages (grazing or harvested), crop residues or byproducts. For finishing systems, IPCC (2006) suggests a Ym of 3.0 ± 1.0 % when diets contain 90 % or more concentrates.

Tier 3 methodology uses country-specific estimates of emission factors derived from models that account for parameters such as diet composition, seasonal variation, and possible mitigation strategies (IPCC 2006; Crosson et al. 2011; Garnsworthy et al. 2012). However, these calculations may not address the variation encountered in commercial production due to variations in feed intake, differences in diet composition and diet characteristics as well as variation surrounding farm system input and output parameters. The inherent uncertainties of emission factors can have important implications for estimated total agricultural emissions reported by a particular country (Bannink et al. 2011; Crosson et al. 2011).

The uncertainty of CH_4 prediction of the IPCC Tier 2 model is estimated to be ± 20% (IPCC 2006), and thus, for Canada's national inventory, the agricultural sector has the highest uncertainty (37%) compared to other sectors (Environment Canada 2010 cited by Alemu et al. 2011). For that reason, the IPCC recommends using a Tier 3 approach to produce more accurate estimates of enteric CH_4 emissions. A Tier 3 approach makes use of local livestock systems production data from monitoring, experiments and validated calculation methods (Bannink et al. 2011).

1.4. Methane from ruminants

1.4.1. Ruminant digestive system

Primary feeds for ruminants are forages and fibrous byproducts, composed mainly of cellulose, a glucose polymer with β-linked bonds that cannot be digested by mammalian digestive enzymes. Ruminants have developed an alternative digestive system with anatomical and physiological adaptations that allow microbial fermentation of feed in the forestomach, prior to digestion and absorption by the animal itself. The ruminant stomach is divided into four compartments, namely the reticulum, rumen, omasum and abomasum. Briefly, the rumen provides a continuous aqueous culture system where feed enters and is then fermented by anaerobic bacteria, protozoa and fungi, producing volatile fatty acids (**VFA**), microbial cells and gases (e.g., CH_4 and CO_2). The volatile fatty acids are mainly absorbed through the rumen wall. The CH_4 is produced by methanogens and together with $CO_{2,}$ is released by eructation. The microbial cells, together with undegraded food components, pass to the omasum, abomasum and small intestine where a portion of them are digested and absorbed (McDonald et al. 2010).

1.4.2. Methanogens

Methanogens belong to the domain *Archaea* and the phylum *Euryarchaeota*. *M*ethanogens are a group of microorganisms characterized as: (1) obligate anaerobes, (2) synthesizing CH_4 as the end product of anaerobic respiration, (3) containing pseudomurein, heteropolysaccharide, or protein in their cell walls instead of peptidoglycan found in the cell walls of bacteria, (4) possessing unique cofactors (e.g., coenzyme M, HS-HTP, coenzymes $F_{420,}$ and F_{430}) and lipids (e.g., isopranyl glycerol ethers), and 5) obtaining energy by converting CO_2, H_2, formate, methanol, acetate and other compounds to either CH_4 or $CH_4 + CO_2$ (McAllister et al. 1996; Prescott et al. 2005; Hook et al. 2010; St-Pierre and Wright 2012; McAllister et al. 2015).

Based on 16S rRNA gene sequences, a novel group distantly related to the Thermoplasmatales (belonging to rumen Cluster C) is abundant in ruminants. However, the majority of ruminal methanogens belong to groups related to

Methanobrevibacter gottschalkii and *Methanobrevibacter ruminantium*. Depending on type of diet fed, the important species of methanogens in the bovine rumen are: *Methanobrevibacter ruminantium* and *Methanosphaera stadtmanae* for lactating dairy cattle fed total mixed rations, *Methanomicrobium mobile*, *Methanobacterium formicicum* and *Methanosarcina barkeri* in grazing cattle, *Methanobrevibacter spp.* detected in cattle housed indoors fed total mixed rations, and *Methanobrevibacter ruminantium*, *Methanobrevibacter thaueri*, *Methanobrevibacter smithii*, and *Methanosphaera stadtm*anae in feedlot cattle fed diets based on corn grain (Hook et al. 2010; Kumar et al. 2014; McAllister et al. 2015).

Methanogens are integrated into the rumen microbial consortia and they are known to have symbiotic relationships with rumen microorganisms (involving interspecies hydrogen transfer), especially with rumen protozoa and fungi where the methanogens can be associated intracellularly and extracellularly. Protozoa possess hydrogenosomes (cellular organelles generating hydrogen) that provide H_2 to methanogens to produce CH_4. Genera of protozoa such as *Entodinium, Polyplastron*, *Epidinium*, and *Ophryoscolex are* most often associated with *Methanobacteriales* and *Methanomicrobiales* methanogens in the bovine rumen (Hook et al. 2010; Leng 2014).

The biological role of methanogens is to avoid the accumulation of hydrogen in the rumen. Excess hydrogen reduces the ability of microbial populations to oxidize the cofactors responsible for electron transfer in the rumen, thus the energy synthesis from fermentation is blocked. Accumulation of hydrogen in the rumen could reduce feed digestibility and animal productivity (Hook et al. 2010; Leng 2014).

1.4.3. Ruminal fermentation

Anaerobic fermentation of organic matter (**OM**) occurs mainly in the rumen. Fermentation can occur in the hindgut, but net contribution to energy supply is small. Anaerobic fermentation results in products that ruminants can (e.g., acetic acid, propionic acid, butyric acid, microbial protein, fatty acids, vitamins) and cannot (e.g., CO_2, CH_4, ethanol; McDonald et al. 2010) use. Fermentation is a complex process that requires synchronization and cooperation of the consortium of anaerobic bacteria and methanogenic archaea (Stams and Plugge 2010). Bacteria, protozoa and fungi are defined as primary digestive microorganisms that hydrolyze proteins, starch and plant cell-wall polymers, producing amino acids and simple carbohydrates. Primary and secondary microorganisms ferment endproducts from primary microorganisms and produce VFA, hydrogen (**H_2**) and CO_2 (Fig 1.4). Methane is then formed by ruminal methanogens using both H_2 (80%) and formate (18%) (McAllister et al. 1996).

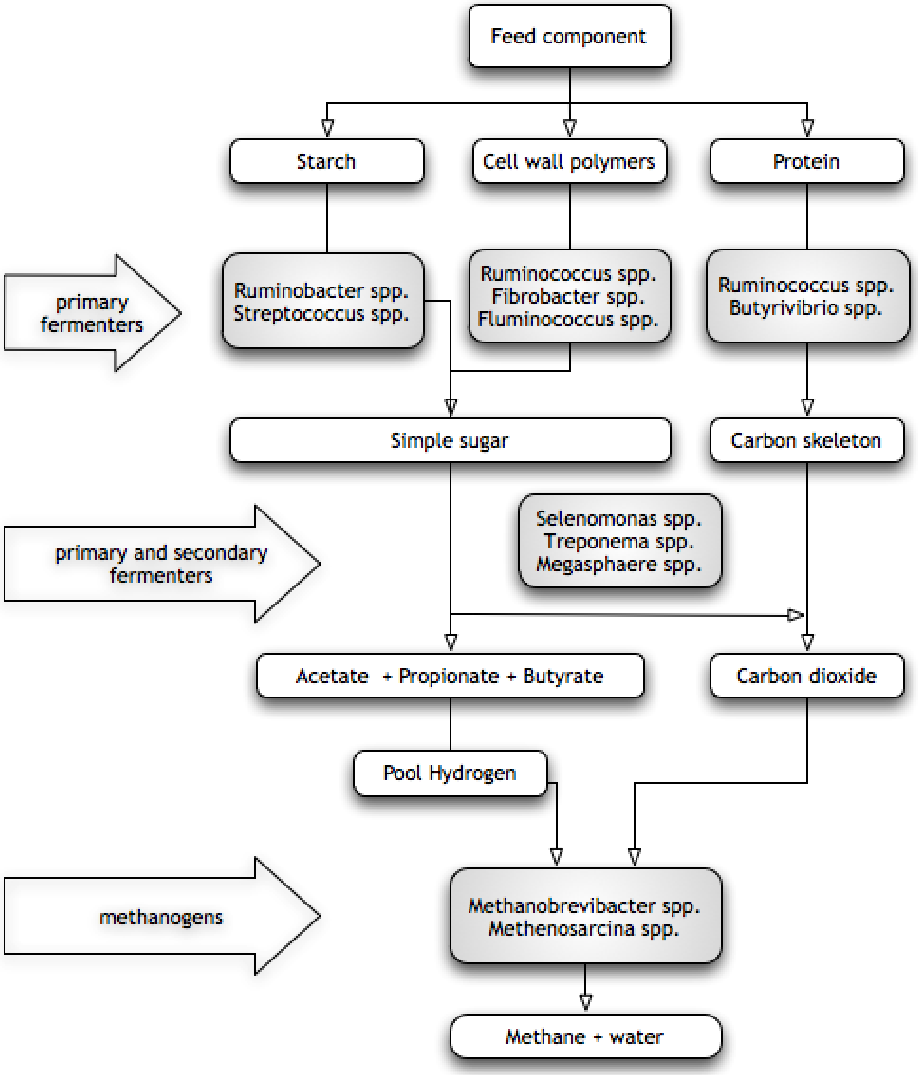

Figure 1.4. General process of rumen fermentation (adapted from McAllister et al. 1996; Sejian et al. 2011)

Energy used by ruminal microorganisms in anaerobic environments comes from substrate oxidation. Fermentation of glucose is an oxidative process under anaerobic conditions occurring using the Embden-Meyerhof-Parnas pathway and generating reduced cofactors like NADH (Fig.1.5). These reduced cofactors must be reoxidized (e.g., NADH to NAD) to complete the fermentation of sugars. Regeneration of NAD+ is accomplished by electron transfer to acceptors other than oxygen (CO_2, sulphate, nitrate, fumarate). Electron transport-linked phosphorylation inside microbial bodies is a means of generating ATP from the flow of generated electrons through membranes, if the required co-factors are present (Moss et al. 2000).

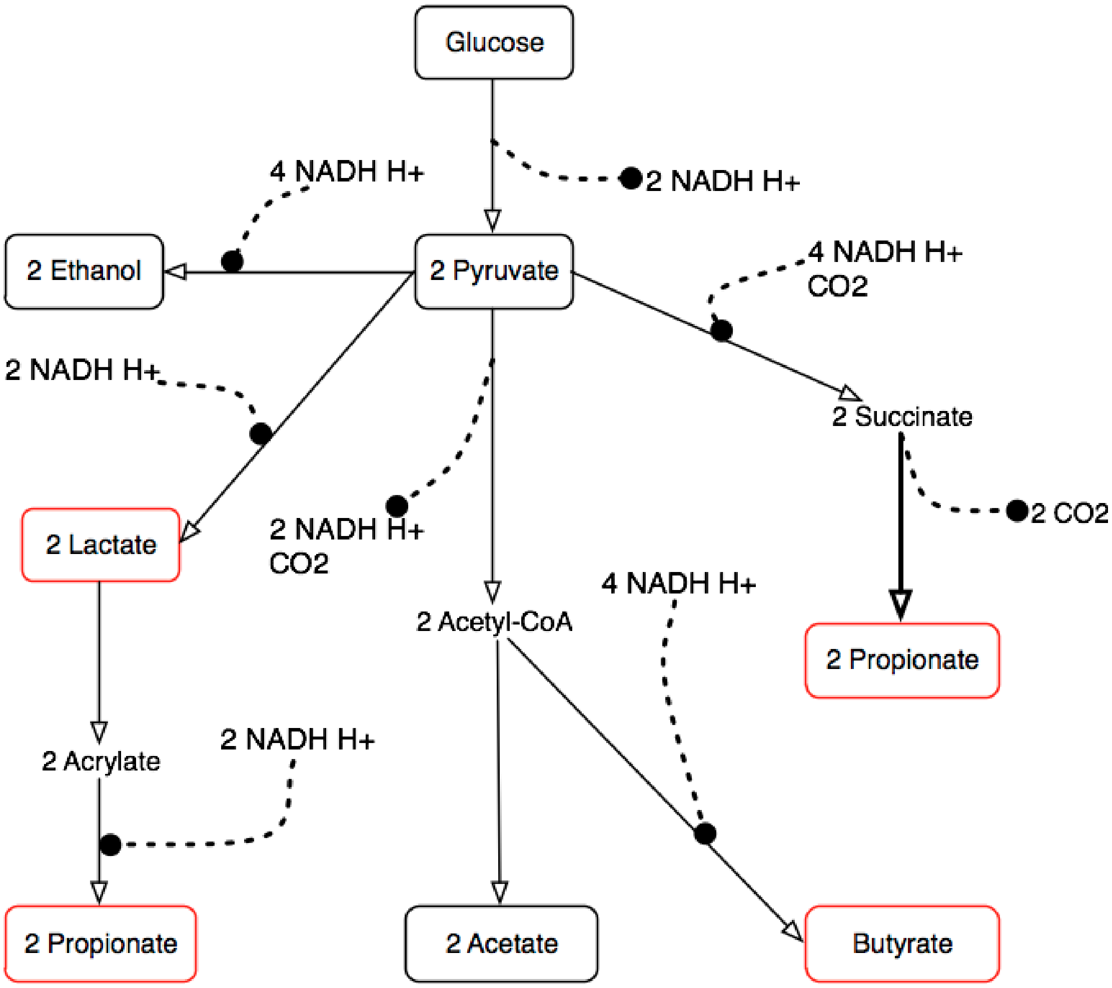

Figure 1.5. A schematic representation of the metabolism of NADH H+ (hydrogen sinks in red boxes; from Moss et al. 2000)

1.4.4. Ruminal methanogenesis

In normal feeding conditions, CH_4 production is a consequence of the microbial fermentation of OM, primarily dietary carbohydrates (e.g., cellulose, hemicellulose, pectin and starch), in the digestive tract of ruminant. It leaves the rumen by eructation representing a loss of energy equivalent to 2 to 12% of total gross energy intake (**GEI**) (Johnson and Johnson, 1995; McDonald et al. 2010; Leng 2014). The process by which ruminal methanogens form CH_4 is called methanogenesis and the essential substrates necessary for ruminal methanogenesis are H_2, formate, methylamines and CO_2 (Moss et al. 2000; Mills et al. 2001; France and Djistra 2005). Most of the H_2 produced during fermentation of carbohydrates is generated during the process of conversion of hexoses to acetate or butyrate via pyruvate. The equations that describe this process are (Knapp et al. 2014):

[1] Glucose → 2 pyruvate + 4H (Embden-Meyerhof-Parnas pathway)

[2] Pyruvate + H_2O → acetate + CO_2 + 2H;

[3] Pyruvate + 4H → propionate + H_2O;

[4] 2 acetate + 4H → butyrate + $2H_2O$ + 2H

Production of metabolic hydrogen **[H]** is a thermodynamically unfavorable process that is controlled by the potential of the electron carrier. In normal ruminal fermentation, methanogenesis is the principal route of re-oxidation reactions, with [H] transferred from the fermentative microbiota to methanogens mainly as H_2. However, production of propionate and butyrate are competitors for [H] and H_2.

Traces of H_2 inhibit the hydrogenase activity through negative feedback mechanisms, and if not removed, will reduce carbohydrate degradation, the rate of microbial growth, and the synthesis of microbial protein. More H_2 is tolerated in the presence of ferridoxin-linked pyruvate oxidoreductases (Moss et al. 2000; McAllister and Newbold 2008; Ungerfeld 2015).

The [H] is converted to H_2 by hydrogenase-expressing bacterial species, and the H_2 is converted to CH_4 by methanogens through the reaction (Knapp et al. 2014):

[5] $CO_2 + 8H \quad \rightarrow \quad CH_4 + 2H_2O$

Typically, 60 to 80% of total CH_4 generated in cattle production comes from the rumen during microbial fermentation of cellulosic feed and the rest is by decomposition of manure (Johnson and Johnson 1995; Vergé et al. 2007). In any case, total CH_4 production is considered an energy loss for ruminants (Rotz et al. 2010; Crosson et al. 2011; Garnsworthy et al. 2012).

The amount of CH_4 produced by ruminants is influenced by many factors including: 1) diet composition and proportion of forage, 2) DMI specially type of carbohydrate intake, 3) digestibility of nutrients, 4) source of grain and how it is processed, 5) rate of passage, 6) rate of ruminal fermentation and rate of methanogenesis, 7) acetate:propionate ratio, 8) type and population of rumen bacteria, 9) management factors such as feeding strategies, and 10) environmental factors such as temperature or stress (McAllister et al. 1996; Beauchemin et al. 2009; Sejian et al. 2011). The effects of DMI, carbohydrate sources, lipids and inhibitors are briefly discussed below because they have direct effects on methane production and most of extant empirical models include these dietary factors (not inhibitors).

1.4.5. Dietary factors that affect methane production

Many dietary factors affect enteric CH_4 production. It is well known that there is greater production of CH_4 from high-forage compared with high-concentrate diets (NASEM 2016). Kriss (1930) established the first linear model that explains the positive relationship between CH_4 and DMI establishing a coefficient of relationships equal to 0.937 ± 0.007. Subsequent research established that DMI increases CH_4 production due to an increment in fermentable OM in the rumen. However, the type of carbohydrate fermented also influences CH_4 production due to impacts on ruminal pH, the microbial population and ruminal endproducts of digestion (Johnson and Johnson 1995). High proportion of forage, and specifically high concentration of fiber increases the proportion of GEI lost as CH_4 (NASEM 2016). The ratio of acetate:propionate is favoured by fermentation of cell wall fiber leading to greater CH_4 losses (Moe and Tyrrell 1979).

Moreover, different forages may produce differences in CH_4 production at similar stages of maturity. For example, cereal forages are more methanogenics than are legumes forages. Additionally, plant maturity is characterized by reductions in soluble sugars and increase in lignification, which increase production of CH_4 compared with immature plants (Johnson and Johnson 1995; Beauchemin et al 2009; NASEM 2016).

There are clear relationships between feed OM digestibility, concentrate feed or starch intake, and the pattern of ruminal fermentation in regard to acetate and propionate production (Hristov et al. 2013). Indeed, production of acetate and butyrate releases hydrogen, whereas propionate serves as a net hydrogen sink. Consequently, diets that increase propionate and decrease acetate in the rumen are often associated with a reduction in ruminal CH_4 production, given that less hydrogen is available to methanogens for reducing CO_2 to CH_4 (Beauchemin et al. 2009). High levels of DMI are usually achieved by feeding greater amounts of concentrate or grain. However, CH_4 production from high grain diets is relatively low because the non-fiber carbohydrate (**NFC**) in the diet causes an increase in the proportion of propionic acid, an increase in rate of passage from the rumen and thus less retention time of feed in the rumen, and less OM fermented in the rumen (Shibata et al. 1993; Beauchemin et al. 2009). As a consequence of reduced retention time in the rumen, the fraction of GEI lost as CH_4 decreases by 1.6% per level of intake (Jonhson and Johnson 1995; Hristov et al. 2013).

Supplementation with fat has been studied extensively for many years. The reduction of CH_4 achieved by fat is due to bio-hydrogenation of unsaturated fatty acids, inhibition of protozoa growth and reduction in fibre digestibility (Johnson and Johnson 1995; Gerber et al. 2013b). However an excess of fats in the diet cause negative effects on feed intake, carbohydrate digestion and alterations in ruminal fermentation, which together have negative consequences on animal production. Due to the high concentration of fat in distillers grain from corn (9 to 10% of dry matter [**DM**]; Hünenberg et al. 2013ab), it has been shown to be an interesting fat source and its inclusion in beef cattle diets decreases CH_4 production (McGinn et al. 2009; Hünenberg et al. 2013ab).

In the last past decades, many studies have tested strategies to mitigate CH_4 production using different types of additives that have specific inhibitory effects on rumen methanogens. Some of them are: use of compounds derived from plants (condensed tannins, saponins, garlic acid, essential oils); organics acids (fumarate, malate); ionophores (monensin), and direct-fed microbials and enzymes. Some products have been shown to decrease CH_4 emissions, but in some case the results have been inconsistent (Hook et al. 2010; Gerber et al. 2013b; NASEM 2016). Electron accepters such as nitrate and sulfate reportedly lower CH_4 reduction; however, feeding nitrate to cattle requires a period of acclimation to prevent toxicity (NASEM 2016). Promising inhibitors such as 3-nitrooxypropanol have been reported to lower CH_4 production in dairy cattle by up to 60% (Haisan et al. 2014), and in beef cattle by 33% in short- and 59% in long- term experiments (Romero-Perez et al. 2014; Romero-Perez et al. 2015; NASEM 2016). Experimental development of 3-nitrooxypropanol as a CH_4 depressor continues.

1.5. Mathematical modeling in animal nutrition

Mathematical modeling is defined as "*the use of equations to describe or simulate processes in a system which inherently applies knowledge and is indispensable for science and societies, especially agriculture*" (Dumas et al. 2008). Animal nutritionists have used modeling extensively over the past century to integrate the knowledge of digestive processes in a way that could predict animal performance.

Very early on, Wood and Yule (1914) asked "*Can one predict with any approach to accuracy what amount of fat, work, or milk will be produced by a diet supplying a known amount of starch equivalent above that required for maintenance?*" mathematical models that numerically represent animal nutrition have been based on statistical analysis and empirical relationships between variables of experimental data. In recent years new approaches such as mechanistic models or models based in process have been used to understand the mechanisms that rule the biological processes of digestion and metabolism. However, this new approach to explaining biological relationships demands complex mathematical expressions, advanced mathematical theory and sophisticated software (France and Kebreab 2008).

Mathematical models are necessary to describe and understand the "how-why-what" of any biological system (McPhee 2009). One purpose of models is to add mathematical and logical consistency to the probable results from an event, phenomenon or observation based on analysis and evaluation of data generated by experiments. The modeling process, or "simulation modeling", can comprise one or many equations integrated in a logical framework using a determinate flux of information (Black 2014).

The study of CH_4 emissions is expensive, technically challenging, as it is difficult to obtain measurements from a large numbers of animals raised under various management conditions. Consequently, mathematical models have been used to estimate CH_4 emissions from ruminants (Kebreab et al. 2009). These models are used to extrapolate the results measured on a small scale (one animal), to the intermediate scale (herd) and to the large scale (country or continent). In general, models have been developed to establish relationships between dietary nutrients and the amount of nutrients in products or excreta, estimate total emissions for inventories and accounting, develop mitigation options, and predict environmental impact of different animal classes. In addition, models have been used to identify the knowledge gaps, raise awareness, encourage adoption, and develop policies (Moraes et al. 2012; Schils et al. 2012).

1.6. Classification and use of models

Thornley and France (1984) cited by McPhee (2009) described a scheme for classifying models (Table 1.2) that is widely recognized as a standard and used extensively by scientists for the modeling of ecological, agricultural, hydrological, and environmental systems.

Table 1.2. Classification of models (Adapted from McPhee 2009).

	Classification	
Dynamic	↔	Static
Deterministic	↔	Stochastic
Mechanistic	↔	Empirical

Baldwin (1995) cited by McPhee (2009) defined each level of classification as follows:

- *Dynamic models*: Models based upon differential equations.
- *Static models*: Models typically algebraic in formula and solved for a specific set of conditions, which exist at a set point in time.

- *Deterministic models*: Models whereby all solutions from an equation or set of equations are exact and each set of input parameters has a predetermined singular outcome.
- *Stochastic models*: Models defined by probability functions, which take into account the variance that is not fully understood; hence the outcome is random within a range of possible outcomes for each input parameter set.
- *Mechanistic models*: Models that assume full knowledge of casual relationships within the system whereby computed results relate to a broad range of realities. The often employ deterministic equations, but can be based on stochastic models.
- *Empirical models*: Models that use existing data to describe the relationship between one or two variables. Care must be applied when extrapolating beyond the limitations of the data. Empirical models are widely used in diverse areas of agriculture (e.g., animal science).

Considering the importance and complexity of environmental evaluation, models are useful for the beef industry for identifying potential impacts of farms on the environment. Thus, models have potential to estimate the effects of dietary interventions used to reduce CH_4 emissions of beef cattle because empirical and mechanistic models should have better prediction accuracy and to improve the representation of relationships between variables and CH_4 compared with the IPCC Tier 2 approach. Moreover, models can be used to quantitatively or dynamically predict enteric CH_4 production in ruminant production systems for regulatory or assessment purposes, create enteric CH_4 mitigation strategies, or document impacts of mitigation strategies (Ellis et al. 2010; Belflower et al. 2012).

Nevertheless, how well these models predict the release of CH_4 or estimate effectiveness of a mitigation strategy is dependent on the accuracy of the mathematical method or equations used. Accurate prediction of CH_4 emission is a requirement for calculating and deriving a realistic estimate of whole farm GHG balance (Ellis et al. 2010).

Models used to predict CH_4 production by cattle can be classified into two main groups:

- *Empirical or statistical models*: These models try to directly relate the nutrient intake of the animal to CH_4 production (Kebreab et al. 2006; Kebreab et al. 2009; Alemu et al. 2011). Within these empirical models many regression equations have been developed to predict CH_4 emissions based on the chemical composition of the diet fed to cattle and/or a description of the animal (e.g., body weight [**BW**]) (Ellis et al. 2010).
- *Dynamic mechanistic models*: These models simulate CH_4 emissions based on a mathematical description of ruminal fermentation biochemistry.

Empirical models have been used as a tool over many years (e.g., Kriss 1930; Bratzler and Forbes 1940; Blaxter and Clapperton 1965; Moe and Tyrrel 1979; Jentsch et al. 2007; Ellis et al. 2007; Ellis et al. 2009; Yan et al. 2009; Ricci et al. 2013; Moraes et al. 2014). In general, these models tend to be practical or simple to use for rapid diet evaluation or for larger-scale GHG inventory purposes. In fact, regression equations are used to relate enteric CH_4 emissions to DMI, energy content of the diet, diet composition, animal characteristics and/or management. Compared with mechanistic models, empirical models use inputs that are easily measured or estimated, and they can approximate emissions using limited information from the animal or diet.

However, empirical models tend to fail or lose accuracy when they are applied outside the data range upon which they were developed. Their simplicity is obtained at the expense of accuracy thereby increasing errors in to national inventories or whole-farm GHG emission estimates (Schils et al. 2012). Nevertheless, their simplicity also allows national calculations because datasets to drive more complex and possibly more accurate models are often not available. Furthermore, most equations are based on comparatively small data sets obtained with specific diet ingredients or ration types (Jentsch et al. 2007). Despite the problems mentioned above, empirical models of CH_4 prediction can be effective tools to identify dietary regimes or specific approaches to reducing methanogenesis (Table 1.3).

Dynamic, deterministic or mechanistic models that represent digestion and metabolism in the rumen such as COWPOLL (Dijkstra et al. 1992) or that represent digestion, metabolism and production of dairy cows such as MOLLY (Baldwin 1995 cited by Kebreab et al. 2008), have been used to determine CH_4 emissions from cattle (Kebreab et al. 2008; Gregorini et al. 2015). These models are based on an understanding of the fundamental biological mechanisms that control a particular biological activity. A mechanistic model is constructed by looking at the structure and analyzing the behavior of the whole system, dividing it into compartments or sections to represent its individual constituents and looking at interactions over time (Dumas et al. 2008; France and Kebreab 2008). Individual experiments can be limited as they demonstrate the effect of individual treatments for a particular animal type and environment. In contrast, mechanistic models are able to extend or extrapolate results by investigating responses outside of the scope of the experiments from which the input data were obtained (Mills 2008).

1.7. Methane prediction models for cattle

Methane production in the rumen is a complex process and in the last decades significant advances have been made in its understanding. The first empirical model used to predict CH_4 production from cattle was developed by Kriss (1930) and represented a linear relationship between CH_4 and DMI. Since this first attempt to predict CH_4 production, numerous models have been developed. Due to the complexity of methanogenesis, models that predict CH_4 have evolved over time towards models that consider more variables or non-linear mathematical expressions (Table 1.3)

Most empirical and mechanistic CH_4 prediction models have been developed for dairy cows as they have a greater feed intake compared with beef cattle (Olesen et al. 2006). Moreover, accurate prediction of CH_4 from most models is poor because the predictions have significant bias and they exhibit deviations from the regression slope when the results are compared with real or observed data (Ellis et al. 2010). Despite these limitations, some of these equations have been incorporated into whole farm emission models without distinguishing between dairy and beef farms. These whole farm emission estimates have then been used in numerous life cycle assessment studies (Del Prado 2013; Table 1.4). Furthermore, some models are used in national inventory methodologies in some countries, despite limited evaluation for accuracy and precision. The environmental impact of beef cattle production and estimation of the effectiveness of particular mitigation strategies are dependent on the accuracy of the mathematical method or equations used. Hence, accurate prediction of CH_4 emission is a requirement to calculate a realistic estimate of whole farm GHG balance and national GHG inventories (Ellis et al. 2010).

Table 1.3. Summary of empirical enteric methane models for cattle.

Author and year	n	Animals used	Variables used for equations to predict methane
Kriss 1930	1	Cows and steers	Based on DMI
Bratzler and Forbes 1940	1	Dairy cows	Based on digested carbohydrates
Axelsson 1949 (cited by Ellis et al. 2007)	1	Dairy cows	Based on DMI
Blaxter and Clapperton 1965	1	Mostly sheep	Based on DE as percentage of maintenance
Moe and Tyrrell 1979	4	Dairy cows	Based on different kinds of fiber in feed
Moe and Tyrrell 1979b	3	Dairy cows	Based on NSC, HC, Cellulose
Holter and Young 1992	7	Dairy cows	Based on milk, % components of milk, diet composition and supplemental dietary fat
Shibata et al. 1993	5	Ruminants	Based on DMI, DE intake and times over maintenance
Kirchgeßner et al. 1995 (cited by Ellis et al. 2010)	4	Dairy cows	Based on CP, CF and NFE and fat/ milk yield and BW
IPCC 1997 Tier 1	1	Cows in general	Fixed value (Dairy, 118; Non dairy, 47 kg CH_4 head yr^{-1} for North America)
IPCC 1997 Tier 2	1	Cows in general	Based on GEI
Corré 2002 (cited by Ellis et al. 2010)	2	Dairy cows	Based on milk yield
Giger-Reverdin 2003	7	Dairy cows	Based on DMI, EE, FA, BW or index of saturation
Mills et al. 2003, linear and non-linear equations	4,3	Dairy cows	Based on DMI, ME, N, ADF, starch, forage proportion, MEI and Starch/ADF ratio
IPCC 2006 Tier 1	1	Cows in general	Fixed value (Dairy, 128; Non dairy, 53 kg CH_4 head yr^{-1} for North America)

IPCC 2006 Tier 2	1	Cows in general	Based on GEI
Schils et al. 2006	2	Dairy cows	Based on intake of concentrate, silage corn and grass
Ellis et al. 2007	32	Dairy cows and beef cows	Based on dietary components and daily intakes of dietary components
Jentsch et al. 2007	6	Different categories	Based on DMI level, BW, $BW^{0.75}$, CP, CF, fiber and N free-extract
Grainger et al. 2007	1	Dairy cows	Based on DMI
Ellis et al. 2009 linear and non linear models	15,15	Beef cows	Based on dietary components and daily intakes of dietary components
Yan et al. 2009	6	Beef cows	Based on different types of energy and ratios between them
Ramin and Huthanen 2012	4	Beef and dairy cattle	Non linear equations based on dietary components
Ramin and Huthanen 2013	26	Ruminants	Based on dietary components and daily intakes of dietary components
Ricci et al. 2013	4	Beef and dairy cattle	Based on GEI, DEI, MEI, DMD, stage of animals and level of the concentrate
Moraes et al. 2014	12	Beef and dairy cattle	Based on GEI, NDF, BW, EE, and MF
Patra 2014, linear and non linear models	14,4	Buffaloes	Based on dietary components and daily intakes of dietary components
Jiao et al. 2014	25	Young Holstein cattle	Based on dietary components and daily intakes of dietary components
Patra 2016, linear and non linear models	18,12	Sheep	Based on dietary components and daily intakes of dietary components
Charmley et al. 2016	2	Beef and dairy cattle	Based on DMI and GEI

Note: n, number of equations developed; DMI, dry matter intake; DE, digestible energy; NSC, non structural carbohydrates; HC, hemicellulose; CP, crude protein; CF, crude fiber; NFE, nitrogen free-extract; BW, body weight; GEI, gross energy intake; VCDMI, volatile corrected dry matter; DM, dry matter; NDF, neutral detergent fiber; EE, ether extract; FA, fatty acids; ME, metabolizable energy; ADF, acid detergent fibre; MEI, metabolizable energy intake; SF_6, sulphur hexafluoride tracer gas technique; DEI, digestible energy intake; DMD, dry matter digestibility; MF, milk fat.

Table 1.4. Some farm models that use equations to predict CH_4 (Adapted from Del Prado et al. 2013)

Model	Country	Production system	CH_4 enteric estimation from:	Type of model	Frequency of calculations	Economics	Scale
ECOMOD-SUITE	Australia, New Zealand	Ruminants	DMI	Mechanistic, dynamic	Daily	No	Farm
HOLOS	Canada	Beef	IPCC 2006 -Tier 2	Empirical	Annual/for livestock monthly	No	Farm, LCA
FASSET	Denmark	Ruminants, monogastric	DM, fibre, fat, protein	Mechanistic, dynamic	Daily	Version 1	Farm
FARMSIM	France	Dairy	IPCC and mechanistic model for grazing	Semi-mechanistic	Daily	No	Farm
FARMGHG	Europe	Dairy	DM, fibre, fat, protein	Empirical	Daily/month	No	Farm
DAIRYWISE	The Netherlands	Dairy	DMI	Empirical	Daily, annual	Yes	Farm
OVERSEER	New Zealand	Ruminants	DMI	Empirical	Monthly	No	Farm
HOOFPRINT	New Zealand	Ruminants	IPPC-Tier 2 (NZ specific)	Empirical	Daily, annual	No	Farm
ISFM	USA	Cattle	DMI; diet energy, fiber and starch.	Dynamic, process simulation	Mostly daily, some monthly, emissions are often hourly	Yes	Whole farm
DAIRY NZ WFM + MOLLY + OVERSEER.	New Zealand	Dairy	Mechanistic	Semi-mechanistic	Daily, annual	Yes	Farm
HOLOSNOR	Norway	Cattle	IPPC (2006)-Tier 2	Empirical	Annual	No	Farm

LAND$_{DAIRY}$+ NGAUGE	Spain	Dairy	IPPC (2006)-Tier 2	Semi-empirical	Daily/monthly	No	Farm
SIMS$_{DAIRY}$	UK	Dairy	DMI, fat intake	Semi-empirical	Daily/monthly	Yes	Farm
DAIRYGEM	USA	Dairy	DMI; diet energy, fiber and starch	Dynamic, process simulation	Mostly daily, some monthly, emissions are often hourly	No	Farm level animal feeding and manure handling
Casey and Holden (2005, 2006)	Ireland	Beef	GE intake; IPCC 1996	Empirical, static	Annual	No	LCA
Foley et al. (2011)	Ireland	Beef	GE intake; IPCC 2006; silage/grazed grass proportions	Empirical, static	Annual	Yes - linked to bioeconomic model	LCA
Lovett et al. (2006, 2008)	Ireland	Dairy	GE intake; IPCC 2006; silage/grazed grass proportions	Empirical, static	Annual	Yes - linked to bioeconomic model	LCA
O´Brien et al. (2011, 2012ab)	Ireland	Dairy	GE intake; IPCC 2006; silage/grazed grass proportions	Empirical, static	Annual	Yes - linked to bioeconomic model	LCA

Note: DMI, dry matter intake; IPCC, Intergovernmental Panel climate change; DM, dry matter; LCA, life cycle assessment; GE, gross energy.

1.8. Model Assessment

Models are abstract, complex mathematical descriptions that are representations, or simulations of natural systems (Tedeschi 2006; Dumas et al. 2008). Mathematical modeling has evolved as a tool useful for policy makers to design and provide new policies or for researchers to express scientific knowledge and new findings (Tedeschi 2006). However, no single model exactly represents this biological system, hence each user must use and interpret a prediction from models considering the uncertainties associated with predictions. Therefore, the evaluation of model adequacy is an essential step in the modeling process because it indicates the level of precision and accuracy of the model predictions (Hamilton 1991; Tedeschi 2006).

A model must be evaluated for its accuracy and precision. In simple words, accuracy is the ability of the model to predict the right value and precision is the ability of the model to predict similar values consistently (Tedeschi 2006). The accuracy and precision of CH_4 prediction models can be evaluated using different statistics methods. Some of them are:

- Mean square prediction error (**MSPE**), which is the unbiased estimator of the variance of the random error.
- Square root of the MSPE (**RMSPE**), expressed as a percentage of the observed mean, giving an estimate of the overall prediction error. The RMSPE can be decomposed into error due to overall bias (**ECT**), error due to deviation of the regression slope from unity (**ER**) and error due to the disturbance (random error) (**ED**) (Bibby and Toutenburg 1977 cited by Ellis et al. 2007).

- Concordance correlation coefficient analysis (***r_c***), described as the reproducibility of paired data sets, can estimate simultaneously accuracy and precision because the estimated correlation coefficient is adjusted by a bias correction factor that indicates how far the regression line deviates from the slope of unity (Tedeschi 2006; Zar 2010).
- Model efficiency (**MEF**), which is the proportion of variation explained by the line formed by the i^{th} model-predicted value. The MEF statistic may be used as an indicator of goodness of fit (Tedeschi 2006).
- The coefficient of model determination (**CD**), which is the proportion of the total variance of the observed values explained by the predicted data (Tedeschi 2006).
- The index of agreement (**IA**), which indicates the sum of the magnitude of the differences between the model-predicted and observed deviations about the observed mean relative to the sum of the magnitudes of the perfect-model ($P_i = O_i$, for all i) and observed deviations about the observed mean (Willmott et al. 2011).

1.9. Summary

The interest in CH_4 started in the 18th and 19th century when this gas was identified as flammable and when it was recognized as an atmospheric gas that was able to retain infrared radiation and exert greenhouse effects. Today, the annual concentration of CH_4 in the atmosphere (approx.1800 ppb) is higher than in the last 800,000 years. In 2014, the Canadian beef industry had 10.2 million beef cattle, and emitted 20 Mt CO_2-eq from enteric fermentation, which is equivalent to 33.8% of total emissions from Canadian agriculture and 1.0% of global emissions from livestock. In ruminants, CH_4 is a natural end product resulting from a fermentative ruminal complex process and is also considered as a loss of energy ranging 2.0 to 12% of GEI. There are multiple factors that affect the amount of CH_4 produced by an animal, such as diet composition. The study of CH_4 emissions is expensive and it is almost impossible to obtain measurements from large numbers of animals raised under various management conditions. Thus, mathematical models have been developed and used to estimate CH_4 emissions from ruminants. For instance, under the terms of the 1997 Kyoto protocol, nations submit an annual national inventory of GHG emissions calculated using methodologies suggested by the IPCC 2006, which generally recommends a Tier 3 methodology to produce more accurate estimates and reduce of uncertainty of enteric CH_4 emissions. However, most of these models have focused on dairy cattle instead of beef cattle, and the models that have been developed for beef cattle have not been evaluated for their accuracy and precision when used outside the limited data from which they were developed. Consequently, there is interest in evaluating existing models for beef cattle, and developing new models that are specific for the various conditions in which beef cattle are raised.

1.10. Hypothesis and objectives

The overall null hypothesis of the thesis research is that calculated values of enteric CH_4 production using available equations are similar to observed values of CH_4. This hypothesis was divided into three components: 1) Predicted values of enteric CH_4 production from extant equations are similar to observed values of CH_4 under different feeding conditions for beef cattle; 2) Predicted values of enteric CH_4 production from new equations are similar to observed values of CH_4 under different feeding conditions for beef cattle and 3) There is no variability in CH_4 predictions from the models when used to predict CH_4 production of beef cattle under Canadian production conditions.

The objectives of the thesis research are to: 1) Evaluate the accuracy and precision of extant enteric CH_4 prediction equations under different feeding conditions, 2) Develop new equations that better account for dietary factors and feed composition and, 3) Compare CH_4 prediction models that account for variables of feed intake and diet composition with IPCC (2006) Tier 2 method on the estimated CH_4 production and emissions factors for beef cattle in Canada.

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CHAPTER 2. An evaluation of the accuracy and precision of methane prediction equations for beef cattle fed high-forage and high-grain diets.[1]

2.1. Introduction

The Global Carbon Project (2013) estimated that total global emission of CH_4 in the period 2000 - 2009 were 0.678 Gt yr^{-1} from natural (51.2%) and anthropogenic (48.8%) sources. Enteric methane produced by cattle during ruminal fermentation contributes to anthropogenic sources; Gerber et al. (2013) estimated that about half of anthropogenic sources are from cattle (0.166 Gt CH_4 yr^{-1}) with beef production contributing 54% of total cattle CH_4 emissions (0.089 Gt CH_4 yr^{-1}).

The Intergovernmental Panel on Climate Change (IPCC 2006) Tier 1 and Tier 2 methodologies use fixed emission factors to estimate CH_4 production from cattle. These methodologies are used by most countries for national inventory of greenhouse gas emissions. Ellis et al. (2010) showed that the accuracy of the IPCC (2006) Tier 2 methodology is low and consequently when used at farm scale this approach could lead to imprecise estimation of CH_4 released. Use of validated prediction equations (Tier 3 approach) could improve accuracy of estimating CH_4 emissions. Prediction equations have been developed specifically for beef cattle (e.g. Ellis et al. 2009, Ricci et al. 2013 and Moraes et al. 2014), but the accuracy of these equations over a range of diet compositions has not been determined using an independent dataset.

Diet has a large effect on the ruminal microbial population, fermentation

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pattern and volatile fatty acid proportions; consequently these variables vary greatly between cattle fed high-forage and high-grain diets (Fernando et al. 2010, McCann et al. 2014). Cattle fed forage diets produce a greater proportion of total volatile fatty acid as acetate, and thus more hydrogen is available for methanogenesis (Janssen, 2010); whereas, cattle fed high-grain diets produce a greater proportion of propionate, high passage rate and thus less hydrogen is available for CH_4 production. Prediction equations derived by regression methods are typically not diet specific and these are limited in their ability to consider the complex interactions between dietary composition and ruminal metabolism. Moreover, most CH_4 prediction equations are not specific for beef cattle fed high-forage or high-grain diets.

We hypothesized that performance of current models used to predict CH_4 production of beef cattle would be different for diets that vary in proportion of forage. The aims of this study were to: 1) construct a database of CH_4 emissions for beef cattle fed forage- and grain-based diets using published literature, and 2) identify the most precise and accurate extant CH_4 prediction models for beef cattle fed diets varying in forage content.

2.2. Materials and methods

2.2.1. Database description

The database was constructed using scientific papers published between 2000 and 2015. The Web of Science (Thomson Reuters, New York, NY) and Papers© v2.8.1 (Mekentosj B.V., Dordrecht, The Netherlands) were used to search for peer-reviewed publications that reported effects of diet on CH_4 production in beef cattle. Published papers were included in the database if they provided a description of the diets and results for CH_4 production (g d^{-1}). The database considered 53 studies representing 207 treatments means (records) for CH_4 production. Details of the studies are provided in Supplementary Table 2.1. Criteria for selecting data to include in the database were: CH_4 production, DMI, dietary ingredients and chemical composition. Data used for the development of already published equations were included in the database, but to avoid model evaluation bias, these development data were excluded when evaluating the equation. This comprised 9.2% of the records for Ellis et al. (2007) and 17.8% for Ricci et al. (2013). Data used by Ellis et al. (2009), Yan et al. (2009) and Ricci et al. (2013) were from local experiments that were not published in peer-reviewed literature.

Missing data on diet composition from publications were estimated from feed tables, by diet formulation software (CPM-Dairy® and Rumnut©) or by calculations from data provided within the paper. Variables in the database were: BW (kg) and proportions (g kg^{-1} DM) of crude protein (**CP**), NDF, acid detergent fibre (**ADF**), NFC, hemicellulose (**HC**), cellulose (**CEL**), fat, sugar, starch, acid detergent lignin (**ADL**), and their respective intakes (kg d^{-1}). Also, included were gross energy (**GE,** MJ kg^{-1} DM), metabolizable energy (**ME**, MJ kg^{-1} DM), GEI (MJ d^{-1}), and metabolizable energy intake (**MEI**, MJ d^{-1}). The response variable was production of CH_4 (g d^{-1}). Measurements of CH_4 that use units other than as grams per day were converted to g d^{-1}.

High dietary forage concentration generally represents diets fed to growing cattle and breeding stock compared with feedlot finishing cattle. Thus, the criterion of dietary forage (g kg^{-1} DM) was used to divide the database into 2 datasets. One dataset comprised treatments with ≥ 400 g kg^{-1} DM dietary forage, the other comprised treatments with ≤ 200 g kg^{-1} DM dietary forage.

2.2.2. Gross energy equations

Equations that included GE were evaluated twice; firstly with observed GE values when reported in the papers (44 studies; records=176) and secondly with GE values calculated (**SIM**) as suggested by NRC (2001) for all papers, omitting the observed values.

2.2.3. Extant prediction equations

Fifty-one extant equations to estimate CH_4 production in beef cattle from 5 studies and IPCC (2006) Tier 2 were evaluated (listed in Supplementary Table 2.2; references given in Supplementary Material 2.1). For IPCC (2006) the CH_4 Ym was 3.0% for diets containing ≥ 900 g kg^{-1} DM concentrate or 6.5% for diets containing < 900 g kg^{-1} DM concentrates. Ellis et al. (2007, 2009) developed equations that consider diet composition variables. Yan et al. (2009) equations are based on contents of energy and DMI. Ricci et al. (2013) equations consider GEI (MJ d^{-1}) and DMI (kg kg^{-1} DM), as well as feed type (1 or 0 according to level of concentrate > or ≤ 500 g kg^{-1} DM diet) and state variables (0 = non-lactating cows; 1 = lactating cows). Moraes et al. (2014) presented separate equations for heifers (**H**) and steers (**S**) with hierarchical levels based only on GEI inclusion (**GEL**; MJ d^{-1}), diet level (**DL**), which included GEI (MJ d^{-1}) and NDF (g kg^{-1} DM), and animal level (**AL**) based on BW (kg), GEI (MJ d^{-1}) and NDF (g

kg^{-1} DM). For steers, equations for GEL and DL were the same (**S-GEL = S-DL**). Models reported by Bratzler and Forbes (1940), Blaxter and Clapperton (1965), Jentsch et al. (2007), Kebreab et al. (2009), Alemu et al. (2011), Bannink et al. (2011) and Ramin and Huhtanen (2013) were not evaluated because the information needed for these equations was not provided in most papers.

Using both datasets, each equation was evaluated within the range of dietary forage proportion used in its development (Table 2.1). Moraes et al. (2014) did not report the range of dietary forage used to develop their equations, therefore the range of proportion of NDF in the diets was used instead. Conditional arguments were used to determine appropriate variable values in the Ricci et al. (2013) and Moraes et al. (2014) equations that consider categorical variables.

Table 2.1. Description of published databases used to develop equations to predict CH_4 in beef cattle.

Source	Dietary variable	Reported Average ($g\ kg^{-1}$ DM)	Min ($g\ kg^{-1}$ DM)	Max ($g\ kg^{-1}$ DM)	Range ($g\ kg^{-1}$ DM)
Ellis et al. (2007)	Forage proportion	790	90	1000	910
Ellis et al. (2009)	Forage proportion	537	90	750	660
Yan et al. (2009)	Forage proportion	819	295	1000	705
Ricci et al. (2013)	Forage proportion	795	90	1000	910
Moraes et al. (2014) - Steers	NDF proportion	358	187	747	560
Moraes et al. (2014) - Heifers	NDF proportion	412	132	783	651

Note: DM= Dry matter

2.2.4. Evaluation of methane equations

Exploratory analyses and overlay plots of the database were performed to reveal the variable distributions. Outliers were identified and excluded by Mahalanobis distance using BW, daily intakes of DMI, NDF, NFC, ADF, fat, starch, GE and CH_4 production. Mahalanobis distance takes into account the correlation structure of the data and the individual scale. From each point to the center of the multivariate normal distribution, Mahalanobis calculate a distance and compare the value with a reference line called the upper control limit. If the distances of each point overpass the upper control limit, the point it is outside of the correlation structure and it is considered an outlier (Kleinbaum et al. 1988; SAS, 2015). Various statistics were used to evaluate goodness of fit of predictions from each equation. Precision and accuracy were evaluated using r_c (Lin, 1989). Evaluation of the prediction error was made by computing the RMSPE, ECT, ER, and ED as suggested by Bibby and Toutenburg (1977). Model efficiency was computed as suggested by Tedeschi (2006).

To obtain bias, residuals were plotted against predicted values for the individual equations. The independent variable of predicted CH_4 production was centered around the mean predicted value before the residuals were regressed on the predicted value (St-Pierre, 2003).

2.2.5 Combined index

Use of numerous statistics to evaluate goodness of fit makes it difficult to rank the performance of equations, because the ranking differs depending on the method used. Thus, a combined index (**CI**) was developed by applying principal component analysis to the matrix formed by all statistical (e.g. adjusted R^2, r_c, RMSPE (g d^{-1}), MSPE, ECT%, ER%, ED% and MEF) values used to assess goodness of fit for each equation. More important principal components (>=1) were selected and rotated by the Varimax method to obtain final communalities for each statistic. The relationships between statistics must be orthogonal to elude overestimation, thus only one statistic was chosen per quadrant ($r_{c,}$ RMSPE (g d^{-1}), ED% and MEF) to create the CI. It is desirable that predictions from each model are accurate and precise (Tedeschi, 2006). Consequently, each model must predict values close to the observed value (higher r_c), with low prediction error (lower RMSPE), large random non-systematic error (higher ED) compared with other error sources, while the model demonstrates efficiency (MEF ≤ 1). For each equation, the value for each of the 4 statistics was adjusted by multiplying by its value of final communality obtained from rotation of components, and then the equations were ranked according to these values from 1 to 51 (from best to worst values) for each statistic, obtaining 4 rankings. The rankings for the 4 statistics were summed to obtain a CI for each equation. Thus, the lowest CI indicates the best performance, and consequently the best equation. The 5 best-fit equations from the analysis of 51 equations using high-forage and high-grain datasets, along with the IPCC (2006) Tier 2 as a reference, are reported herein. Ranking of the best 30 equations for each dataset are provided in Supplementary Tables 2.3 (high-forage diets) and 2.4 (high-grain diets).

2.3. Results

2.3.1. Datasets

The complete database (n = 207) was divided into 2 datasets, based on high-forage (≥ 400 g kg^{-1} dietary forage DM content, n = 151) and high-grain (≤ 200 g kg^{-1} dietary forage DM content, n = 50) content. The mean, standard deviation (**SD**), minimum and maximum values for the variables are presented in Table 2.2. Six treatment means were excluded because they were considered to represent transition diets (210 to 390 g kg^{-1} of dietary forage content DM basis). Twenty-one treatment means were excluded because they were from studies where animals were fed restrictively or additives for CH_4 mitigation were fed. Moreover, 22 treatment means (19 high-forage treatments and 3 high-grain treatments) were excluded because they were identified as outliers by Mahalanobis distance. The total treatments were 116 for high-forage and 42 for high-grain dataset.

The high-forage dataset had an average BW of 406 kg and 717 g kg^{-1} dietary forage DM content compared with a BW of 488 kg and 95 g kg^{-1} DM from forage for the high-grain dataset (Table 2.2). The DMI in the high-forage dataset was lower than in the high-grain dataset (7.6 vs. 8.6 kg d^{-1}, respectively), and as expected forage intake was greater for the high-forage than high-grain dataset (5.3 vs. 0.8 kg DM d^{-1}, respectively). Mean NDF and ADF contents for the high-forage dataset were 386 and 233 g kg^{-1} DM, respectively, compared with 185 and 90 g kg^{-1} DM, respectively, for the high-grain dataset. Fat and starch contents for the high-forage dataset were 36 and 212 g kg^{-1} DM, respectively, and lower than those of the high-grain dataset with 45 and 480 kg^{-1} DM, respectively. The CH_4 production was superior for the high-forage compared with the high-grain dataset (159 vs. 148 g d^{-1}, respectively).

Table 2.2. Summary of nutrient profiles and CH$_4$ emissions for the high-forage and high-grain datasets used to evaluate the models.

	High-forage dataset (n=116)				High-grain dataset (n=42)			
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max
BW (kg)	406	129	107	825	488	113	318	696
Forage proportion (g kg^{-1} DM)	717	188	400	1000	95	23	20	166
DMI (kg d^{-1})	7.6	2.1	3.6	15.1	8.6	1.7	5.4	12.3
Forage intake (kg d^{-1})	5.3	1.8	1.9	11.1	0.8	0.3	0.2	1.8
CP (g kg^{-1} DM)	148	34	59	290	151	32	119	231
NDF (g kg^{-1} DM)	386	99	216	688	185	64	116	473
ADF (g kg^{-1} DM)	233	74	50	432	90	39	35	277
NFC (g kg^{-1} DM)	373	116	79	635	585	91	281	700
HC (g kg^{-1} DM)	153	54	52	313	95	34	49	196
CEL (g kg^{-1} DM)	195	64	10	346	72	35	24	254
Fat (g kg^{-1} DM)	36	14	9	86	45	19	15	110
Sugar (g kg^{-1} DM)	69	41	21	280	45	18	5	93
Starch (g kg^{-1} DM)	212	146	3	536	480	106	113	617
Lignin (g kg^{-1} DM)	38	17	6	107	18	7	9	34
[1]GE (MJ kg^{-1} DM)	16.4	5.4	0.0	20.4	18.4	1.4	14.2	20.5
[2]GE (MJ kg^{-1} DM)	18.1	0.7	16.3	20.3	18.8	1.1	15.8	20.7
ME (MJ kg^{-1} DM)	9.8	1.6	5.4	13.6	12.5	1.5	8.5	15.4
Methane (g d^{-1})	159	60	51	322	148	64	51	295

Note: DMI, dry matter intake; NFC, non fiber carbohydrate; HC, hemicellulose; CEL, cellulose; GE, gross energy; ME, metabolizable energy.

[1] GE values from the original studies.

[2] GE simulated values using NRC (2001) formula for GE.

2.3.2. Equations evaluated with a high-forage dataset

The 5 best-fit equations for the high-forage dataset ranked using the CI are presented in Table 2.3. IPCC (2006) Tier 2 ranked first (CI=24). Three equations from Moraes et al. (2014) outperformed the other equations; equation S-AL ranked second (CI=39; Moraes et al. 2014), SIM S-AL ranked third (CI=44; Moraes et al. 2014), S-GEL ranked fourth (CI=53; Moraes et al. 2014) and N ranked fifth (CI=56; Ellis et al. 2009).

Values for r_c were > 0.7 for equations IPCC (0.715) and S-AL (0.725), with slightly lower values obtained for equations SIM S-AL (0.646), S-GEL (0.678) and N (0.601). Lower RMSPE (g d^{-1}) was obtained for equation N (35.6) and IPCC (39.8). Equations S-AL, SIM S-AL and S-GEL had RMSPE values > 40 (g d^{-1}). Also, RMSPE (%) was lower for equations N (23.9) and IPCC (25.0). Random error for all 5 equations was the principal source of error. The ED computed for equation IPCC (98.7%) was slightly greater than that obtained for SIM S-AL (94.5%), and notably greater than that obtained for S-AL (87.2%), S-GEL (81.8%) and N (76.4%). With the exception of IPCC and SIM S-AL, the error from overall bias of prediction (ECT%) was low (< 2.0%) for the best-fit equations.

Table 2.3. Summary of the 5 best-fit CH_4 prediction equations using the high-forage dataset ranked by combined index.

N	Source	$R^{2adj.}$	r_c	C_b	RMSPE ($g\ d^{-1}$)	RMSPE (%)	ECT %	ER %	ED %	MEF	CI	Ranking
1	IPCC (2006) Tier 2	0.560	0.715	0.95	39.8	25.0	1.2	0.0	98.7	0.56	24	1
50	Moraes et al. (2014) S-AL	0.626	0.725	0.90	42.9	26.5	8.9	3.9	87.2	0.59	39	2
56	Moraes et al. (2014) SIM S-AL	0.532	0.646	0.87	45.9	28.6	1.8	3.1	94.5	0.52	44	3
46	Moraes et al. (2014) S-GEL	0.612	0.678	0.86	45.8	28.4	12.8	5.4	81.8	0.53	53	4
29	Ellis et al. (2009) N	0.587	0.601	0.77	35.6	23.9	9.3	14.3	76.4	0.47	56	5
	Average	0.583	0.673	0.87	42.0	26.5	6.8	5.4	87.7	0.53		

Note: AL, animal level; C_b, bias factor; CI, combined index; ECT%, error due to overall bias of prediction as percentage of mean square prediction error (MSPE); ED%, random or disturbance error as percentage of MSPE; ER%, error due to deviation of the regression slope from unity as percentage of MSPE; GEL, gross energy level; MEF, model efficiency; N, ordinal number assigned to each equation; $R^{2adj.}$, adjusted coefficient of determination; r_c, concordance coefficient correlation; RMSPE, root mean square prediction error; S, steers; SIM S-AL, calculated gross energy for animal level equations.

Table 2.4. Evaluation of bias for the best-fit CH_4 prediction equations using the high-forage dataset.

N	Source	Average CH_4 ($g\ d^{-1}$)	Mean bias ($g\ d^{-1}$)	P value mean bias	Linear bias ($g\ d^{-1}$)	P value linear bias	Maximum bias ($g\ d^{-1}$)	Minimum bias ($g\ d^{-1}$)
1	IPCC (2006) Tier 2	163.5	-4.42	ns	0.01	ns	-2.1	-5.7
50	Moraes et al. (2014) S-AL	156.6	13.02	**	0.19	ns	40.5	-4.1
56	Moraes et al. (2014) SIM S-AL	154.1	6.30	ns	0.20	ns	35.4	-11.1
46	Moraes et al. (2014) S-GEL	153.0	16.60	**	0.25	*	47.9	-2.1
29	Ellis et al. (2009) N	138.0	11.64	**	0.57	**	72.7	-23.7
1	IPCC (2006) Tier 2	163.5	-4.42	ns	0.01	ns	-2.1	-5.7

Note: AL, animal level; SIM S-AL, calculated gross energy for animal level equations; GEL, gross energy level; N, ordinal number assigned to each equation; S, steers; SIM S-AL, calculated gross energy in animal level equations.
*, $P < 0.05$; **, $P < 0.01$; ns, not significant.

Values of MEF obtained for the best-fit equations were < 1, with relatively similar values for all 5 equations (0.56, 0.59, 0.52, 0.53 and 0.47 for IPCC, S-AL, SIM S-AL, S-GEL and N, respectively). Mean biases were significant for equations S-AL, S-GEL and N ($P < 0.01$; Table 2.4). Equations with significant linear bias were S-GEL ($P < 0.05$) and N ($P < 0.01$) with a maximum bias of -2.1, 40.5, 35.4, 47.9 and 72.7 g CH_4 d^{-1} at the maximum predicted value of 326.3, 304.8, 302.5, 277.2 and 245.9 g CH_4 d^{-1}, respectively and a minimum bias of -5.7, -4.1, -11.1, -2.1 and -23.7 g CH_4 d^{-1} at the minimum predicted value of 77.8, 64.3, 65.5, 78.7 and 75.6 g CH_4 d^{-1}, respectively. Plots of the regression residuals on centered predicted values of CH_4 with density shadowing at 95% for each equation is presented in Figure 2.1, where an intercept equal to 0 and a slope equal to 1 indicate absence of bias.

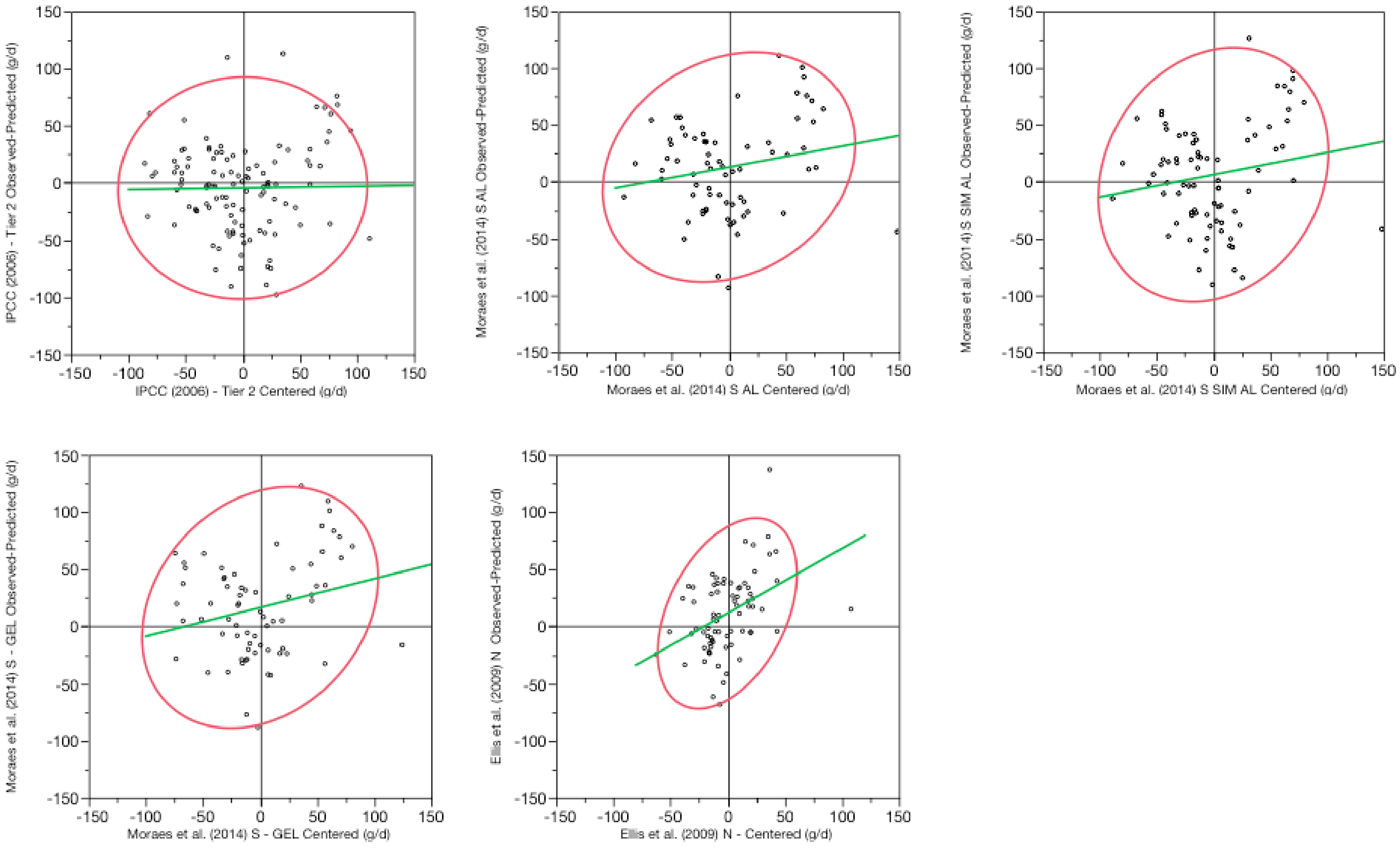

Figure 2.1. Plots of observed minus predicted CH_4 production (g d^{-1}) versus centered CH_4 production for various CH_4 prediction equations using the high-forage dataset. The ellipse indicates the shadow density at 95%, the solid line indicates the regression, and absence of bias occurred when intercept was equal to 0.

2.3.3. Equations evaluated with a high-grain dataset

The ranking of best-fit equations (Table 2.5) using the high-grain dataset differed substantially from the ranking of equations for the high-forage dataset (Table 2.3). Equations IPCC (2006) Tier 2, S-AL, SIM S-AL, S-GEL (Moraes et al. 2014) and N (Ellis et al. 2009) that ranked high for the high-forage dataset were less accurate and precise when they were used with the high-grain dataset. Best-fit equations for the high-grain diets were I (CI=24; Ellis et al. 2009), GEI (CI=24; Ricci et al. 2013), S-GEL/S-DL (CI=26; Moraes et al. 2014), S-AL (CI=37; Moraes et al. 2014), and S-SIM GEL (CI=37; Moraes et al. 2014). On average, these equations had smaller r_c (0.421), greater ED (89.2%), smaller MEF (0.29) and greater RMSPE (55.6 g d^{-1}) values than those for the high-forage dataset. The r_c values were intermediate for equations I (0.445), S-GEL/S-DL (0.406) and S-SIM GEL (0.521), and lower for GEI (0.354) and S-AL (0.376) equations.

The principal source of error for the best-fit equations tested with the high-grain dataset was ED, as was observed for high-forage diets, and the proportion of error attributed to ED was similar (mean, 87.7 vs. 89.2%, respectively). The error attributable to ECT was less by -2.2%, and conversely, ER error was greater by 1.6% for the high-grain compared to the high-forage dataset. The average MEF of the best-fit equations was 0.29, which was lower than the MEF value computed for the best-fit equations for the high-forage (0.53) dataset.

The IPCC Tier 2 equation was ranked 43th with low r_c (0.117), high RMSPE (85.01%), lower MEF (-0.78) and high proportion of ECT (35.1%) instead of random sources (54.1%), but means biases were not observed (Table 2.6). Significant linear bias was only observed for equation S-SIM GEL (*P* < 0.05).

Plots of the regression of residuals on centered predicted values of CH_4 and the shadow density at 95% for each equation are presented in Figure 2.2. Absence of bias occurred when the intercept was equal to 0.

Table 2.5. Summary of the 5 best-fit CH_4 prediction equations using the high-grain dataset ranked by combined index.

N	Source	$R^{2adj.}$	r_c	C_b	RMSPE (g d^{-1})	RMSPE (%)	ECT %	ER %	ED %	MEF	CI	Ranking
24	Ellis et al. (2009) I	0.163	0.445	0.84	62.9	41.9	2.3	0.2	97.5	0.26	24	1
42	Ricci et al. (2013) GEI	0.235	0.354	0.93	47.4	32.3	3.6	0.1	96.3	0.25	24	2
46	Moraes et al. (2014) S-GEL/S-DL	0.294	0.406	0.71	56.3	45.4	6.0	2.7	91.3	0.27	26	3
50	Moraes et al. (2014) S-AL	0.204	0.376	0.66	57.4	46.3	7.8	4.0	88.2	0.24	37	4
52	Moraes et al. (2014) S-SIM GEL	0.625	0.521	0.67	53.9	34.9	3.4	27.8	72.5	0.44	37	5
	Average	0.304	0.421	0.76	55.6	40.2	4.6	7.0	89.2	0.29		
1	IPCC (2006) Tier 2	0.011	0.117	0.62	85.01	57.3	35.1	10.8	54.1	-0.78	169	43

Note: C_b, bias factor; CI, combined index; DL, dietary level; ECT%, error due to overall bias of prediction as percentage of mean square prediction error (MSPE); ED%, random or disturbance error as percentage of MSPE; ER%, error due to deviation of the regression slope from unity as percentage of MSPE; GEI; gross energy intake; MEF, model efficiency; N, ordinal number assigned to each equation; $R^{2adj.}$, adjusted coefficient of determination; r_c, concordance coefficient correlation; RMSPE, root mean square prediction error; S, steers.

Table 2.6. Evaluation of bias for the best-fit CH_4 prediction equations using the high-grain dataset.

N	Source	Average CH_4 (g d^{-1})	Mean bias (g d^{-1})	*P* value mean bias	Linear bias (g d^{-1})	*P* value linear bias	Maximum bias (g d^{-1})	Minimum bias (g d^{-1})
24	Ellis et al. (2009) I	140.4	9.59	ns	-0.06	ns	5.6	15.4
42	Ricci et al. (2013) GEI	158.8	-12.11	ns	0.65	ns	13.7	-67.4
46	Moraes et al. (2014) S-GEL/S-DL	165.8	-13.82	ns	0.32	ns	5.0	-28.0
50	Moraes et al. (2014) S-AL	136.0	16.01	ns	0.44	ns	38.8	-1.7
52	Moraes et al. (2014) S-SIM GEL	161.9	-11.27	ns	1.02	**	38.3	-76.4
1	IPCC (2006) Tier 2	97.9	50.38	***	-0.70	**	-47.9	81.1

Note: N, ordinal number assigned to each equation; DL, dietary level; GEI, gross energy intake; S, steers.
**, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

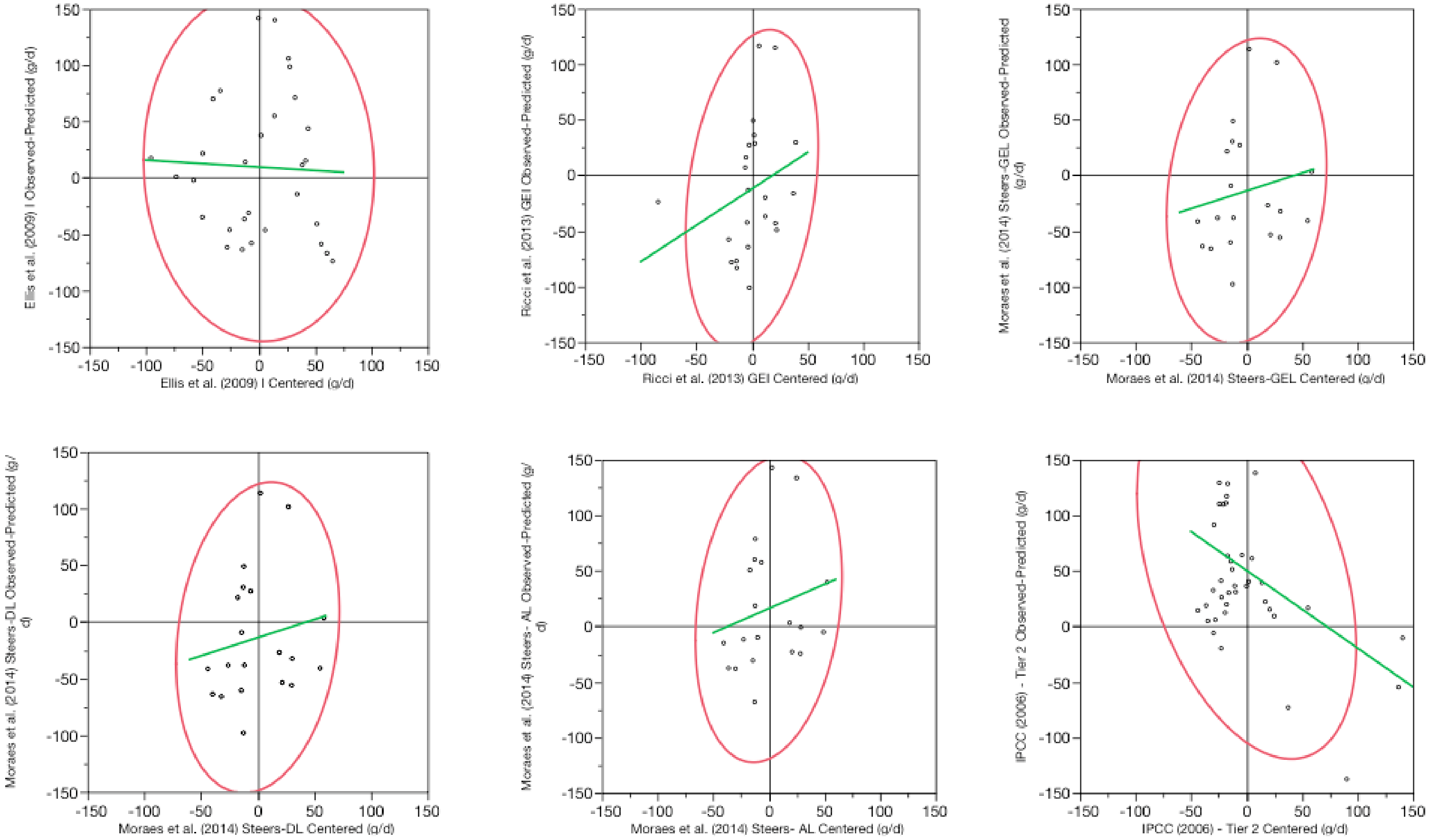

Figure 2.2. Plots of observed minus predicted CH_4 production (g d-1) versus centered CH_4 production for various CH_4 prediction equations using the high-grain dataset. The ellipse indicates the shadow density at 95%, the solid line indicates the regression, and absence of bias occurred when intercept was equal to 0.

2.4. Discussion

The 51 extant equations evaluated were from a relatively small number (i.e. 5) of studies. Although their data used for development were not re-utilized, potential correlation within and among studies may have occurred because the diets used in equation development were similar in nutritional dietary contents and intakes. However, only databases used by Ellis et al. (2007) and Ricci et al. (2013) shared common data (n=90, 20 studies), and although the Ricci et al. (2013) database was larger than Ellis's, the common data represented 46.4% of the total data. Despite commonality of data, the prediction equations from those two studies used different approaches and generally did not share common variables. Ellis et al. (2009), Yan et al. (2009) and Moraes et al. (2014) developed equations from independent databases. There were similarities in dietary characteristics and intakes among the databases used by Ellis et al. (2007 and 2009), Yan et al. (2009), Ricci et al. (2013), Moraes et al. (2014, Heifer and Steer) and our high-forage dataset, as indicated by the ranges for the variables. The SD for daily nutrient intakes (DMI, NDF, ADF, starch and fat) indicated that ranges overlapped among the databases used in the various studies even though the means were not the same across the databases. For instance, mean NDF intake (kg d^{-1}) in the database used by Ellis et al. (2009) was less than for our high-forage dataset (2.22 vs. 2.82 kg d^{-1}, respectively) but the range of ±1 SD indicates that the high-forage dataset included the range used in Ellis et al. (2009) (1.84 to 3.78 vs. 1.51 vs. 2.93 kg d^{-1}, respectively). Similarity in range of nutrient intakes among the various studies indicates that the high-forage dataset was appropriate for evaluating these equations. Additionally, any common data between the high-forage dataset and the data used to develop a particular extant equation was excluded to eliminate bias in evaluating these equations.

The exclusion of treatment means from studies that used feed additives to mitigate CH_4 and/or restrictive feeding was necessary because the effects of additives are not accounted for by extant prediction equations and enteric CH_4 production is affected by restriction of DMI.

As expected mean dietary NDF content and intake were lower for the high-grain (185 g kg^{-1} DM, 1.59 kg d^{-1}) versus high-forage dataset (386 g kg^{-1} DM, 2.93 kg d^{1}). Furthermore, mean NDF content (g kg^{-1} DM) of the high-grain dataset was less than for the other databases (470, Ellis et al. 2007; 326, Ellis et al. 2009; 491, Yan et al. 2009; 444, Ricci et al. 2013; 358, Moraes et al. 2014 steers; and 412, Moraes et al. 2014 heifers). Similarly, dietary ADF content (g kg^{-1} DM) was less for the high-grain dataset (90) than for the other studies (312, Ellis et al. 2007; 184, Ellis et al. 2009; 288, Yan et al. 2009; 270, Ricci et al. 2013; 216, Moraes et al. 2014 steers; and 246, Moraes et al. 2014 heifers).

As intended, the high-grain dataset was characterized by greater mean dietary NFC content and NFC intake (585 and 5.03 vs. 373 g kg^{-1} DM and 2.83 kg d^{-1}, respectively) and starch (480 and 4.13 vs. 212 g kg^{-1} DM and 1.61 kg d^{-1}, respectively) compared with the high-forage dataset. These differences in dietary contents can influence CH_4 production. Indeed, the high-grain dataset was characterized by lower production of CH_4 (148 g d^{-1}) than was the high-forage dataset (159 g d^{-1}). As CH_4 production is affected by intake and nutrient content of the diet, the performance of the various prediction equations differed according to the dataset used.

2.4.1. Performance of equations evaluated with a high-forage dataset

Performance of CH_4 prediction equations was evaluated specifically for diets containing ≥ 400 g kg^{-1} dietary forage content because high-forage diets have greater proportion of fiber and lower proportion of NFC, promoting acetate production in the rumen, which favors methanogenesis (Kebreab et al. 2006).

The best-fit equations for the high-forage dataset had on average greater r_c and MEF, and lower RMSPE than the remaining equations indicating appropriate accuracy and precision when equations were applied to the high-forage dataset. The greater r_c value for IPCC Tier 2 and S-AL (0.715 and 0.725) indicated these equations were more sensitive to predicting CH_4 than the other equations. However, Moraes et al. (2014) reported a RMSPE for equation S-AL (15.1%), which was lower than the RMSPE computed for that equation with real (observed) and simulated values of GEI in the present study (26.5 and 28.6%). This greater prediction error is likely because the high-forage dataset used in the present study represented a wider range of experiments from diverse countries accentuating the variability of each variable.

Dry matter intake is generally positively associated with CH_4 (Beauchemin et al. 2009; Shibata et al. 2010), but by itself is not necessarily associated with ruminal acetate fermentation and thus may fail to accurately predict CH_4 production, especially when diets contain highly digestible carbohydrates. For the top 5 equations, DMI is only considered by the IPCC (2006) Tier 2 model. The variables BW and GEI were considered in equation S-AL and SIM S-AL and only GEI was considered in equation S-GEL (Moraes et al. 2014). However, IPCC (2006) indirectly uses GEI, because it multiplies GE content (18.5 MJ kg^{-1} DM) by DMI. Dietary fiber associated with acetate production and starch associated with propionate production was considered by equation N (Ellis et al. 2009) as starch/NDF (kg d^{-1}). This parameter value is lower than 1 and thus has less impact on estimating CH_4 than NDF alone. Additionally, this factor adjusts the other components of equation N based on DMI. The r_c computed for equation N (0.601) was greater than originally reported (0.598). Conversely, the RMSPE of 23.9% for equation N (Ellis et al. 2009) obtained in our study was smaller than originally reported (30.8%). Better performance of N in our study is attributed to the positive relationship between NDF and DMI on CH_4, the ED computed for equation N was lower than obtained by Ellis et al. (2009) (76.4 vs. 95.8%, respectively). Fat content of diets, which is associated with lower CH_4 production (Martin et al. 2009), was not considered by any of the best-fit equations, but may be indirectly considered by equations that include GEI, when GE content is measured directly on feeds rather than assumed to be constant, because feeds vary in fat concentration.

2.4.2. Performance of equations evaluated with a high-grain dataset

Given that feedlot cattle in North America are fed high-grain diets (≤ 200 g kg^{-1} forage dietary content), the performance of extant equations was evaluated using a high-grain dataset. High-grain diets promote fermentation of non-structural carbohydrates and propionate production that provides a competitive pathway for hydrogen use in the rumen thereby decreasing CH_4 production (Johnson and Johnson, 1995; Beauchemin et al. 2009).

The best-fit equations for the high-grain dataset had on average lower r_c (0.421) and MEF (0.29) and greater RMSPE (40.2%) than the best-fit equations tested with the high-forage dataset indicating less accuracy and precision of equations applied to the high-grain dataset. This reduced equation performance likely originates from the difference in range of dietary forage content originally used to develop the equations (i.e., high-forage diets) compared with the high-grain dataset with which they were tested. Also, the best-fit equations using the high-grain dataset were different than those using the high-forage dataset, indicating that variables used in equations to predict CH_4 in high-grain diets should be different than variables used in equations to predict CH_4 in high-forage diets.

Ricci et al. (2013), using physiological stage and levels of concentrate (> or ≤ 500 g kg^{-1} DM) as correction factors, showed that precision of CH_4 predictions was improved when GEI was included as a principal predictor of CH_4. However, with the high-grain dataset, DMI and energy content of feed (GE or ME) were not associated with increased CH_4 production for high-grain diets. High-grain diets have high energy content because fiber components are replaced by starch and fat (Table 2.2), which both cause changes in ruminal fermentation and a reduction in CH_4 production (Beauchemin et al. 2009; Cottle et al. 2011). Equation I does not consider GEI as a predictor, but instead considers MEI (MJ d^{-1}). Additionally, equation I includes CEL as a positive predictor, with HC and fat as a negative predictors. Consequently, the accuracy and precision of this equation was greater than the other equations that consider GEI, NDF, forage proportion and BW. Jentsch et al. (2007) reported that the fiber components HC and CEL have a positive impact on CH_4 production. However, this effect was not completely observed in equation I because it considers only MEI and CEL as positive predictors of CH_4 with HC and fat as suppressors of CH_4 production.

2.4.3. Performance of IPCC (2006) Tier 2 equation

The IPCC was established by the United Nations Environmental Programme and the World Meteorological Organization in 1988 to assess information relevant for the understanding of human induced climate change, its potential impacts, and options for mitigation and adaptation. In 2006, IPCC released a Tier (1, 2 and 3) methodology for calculating national CH_4 inventories from livestock. Specifically, Tier 2 assumes that 6.5% ± 1% of GE intake is converted to CH_4 for cattle fed forage based diets and 3% ± 1% of GE intake is converted to CH_4 for feedlot cattle fed diets containing $\geq$ 900 g kg^{-1} DM concentrates. Because of wide adoption of the IPCC (2006) approach, the performance and relative ranking of the Tier 2 equation was presented as a reference.

Despite its relative simplicity, the performance of the IPCC Tier 2 equation ranked first for the high-forage diets. It had similar r_c (0.715), RMSPE (25.0%) and MEF (0.56), but greater ED (98.7%), when compared with other more complex equations that consider dietary composition. The relatively strong performance of the IPCC (2006) Tier 2 equation for high-forage diets may reflect that the Ym used (6.5%) originated from a wide range of diets with a large proportion of forage. In contrast, for high-grain diets, the IPCC Tier 2 equation ranked 43th indicating that the Ym used by the IPCC Tier 2 model may not be appropriate for diets with a low proportion of forage (≤ 200 g kg^{-1}). It should be acknowledged that because of the limited availability of data for feedlot cattle fed diets containing ≥ 900 g kg^{-1} concentrate DM, the high-grain dataset included diets containing ≥ 800 g kg^{-1} concentrate DM. It is likely that the CH_4 conversion factor for diets with intermediate forage content is overestimated by IPCC (2006; i.e., > 3 but < 6.5). Our results are consistent with Ricci et al. (2013) who reported that the IPCC (2006) equation predicted 26% more CH_4 than equations they developed using a database of diets containing > 500 g kg^{-1} dietary concentrate DM.

2.5. Conclusions

Current models may give inaccurate values of CH_4 production when used for beef cattle fed diets ranging in proportion of forage, particularly for high-grain diets. Thus, choice of equation used to estimate CH_4 production for beef cattle must be based on the type of diet (e.g., specific for high-forage or high-grain diets, respectively). Use of an inappropriate model may introduce substantial error into CH_4 emission prediction and hence lead to incorrect computation of greenhouse gas inventories or inappropriate mitigation recommendations. In addition to using the appropriate model, primary data for feed intake and diet composition are needed to generate accurate estimates of CH_4 production. The limited availability of CH_4 production data for cattle fed high-grain diets restricts the development and assessment of accurate CH_4 prediction models for feedlot operations.

Supplementary Table 2.1. Summary of studies included in the complete database.

Author(s)	Animal category	Breed	CH_4 measurement method	$CH_4{}^1$ (g d^{-1})	Treatment description
Beauchemin and McGinn (2005)	Steers	Angus	Chambers	62.1	Barley and corn grain in different proportions
Beauchemin and McGinn (2006a)	Heifers	Angus	Chambers	141.5	Forage and grain in different proportions and unrestricted and restricted intake levels
Beauchemin and McGinn (2006b)	Steers	Angus	Chambers	108.0	Lipids, fumaric acid, spice extract, high proportion of forage and high proportion of grain under restricted feeding
Beauchemin et al. (2007a)	Steers	Angus	Chambers	119.6	Different sources of lipids
Beauchemin et al. (2007b)	Steers / heifers	Angus	Chambers	98.7	Different concentration of Quebracho tannins
Boadi and Wittenberg (2002)	Heifers	Holstein and Charolais × Simmental	SF_6	127.6	Different qualities of diets assessed as IVOMD
Boadi et al. (2001)	Steers	Red Angus	SF_6	169.1	Different proportions of alfalfa, bromegrass pastures with barley
Boadi et al. (2004)	Steers	Continental × British crossbred	SF_6	59.4	Different proportions of forage and grain
Boland et al. (2013)	Heifers	Limousin	SF_6	127.0	Availability of herbage mass
Chaves et al. (2006)	Heifers	Angus	SF_6	150.9	Grazing different types of alfalfa or grass pasture
Chung et al. (2013)	Heifers	Crossbred	Chambers	90.0	Proportions of alfalfa and sainfoin at different stages of maturity
Chung et al. (2011)	Steers	Holstein	SF_6	261.0	Different yeast strains (*Sacharomyces cerevisiae*)
Chung et al. (2013)	Heifers	Crossbred	Chambers	90.0	Proportions of alfalfa and sainfoin at different stages of maturity
Cooprider et al. (2011)	Steers	Angus cross steers	Chambers	281.8	Conventional management (estrogen+monensin+others) vs management without antibiotics,

					estrogenic hormones and others
Doreau et al. (2011)	Bulls	Blond d'Aquitaine	SF_6	62.3	Different diets of corn grain, grass hay and corn silage
Dos Santos Pedreira et al. (2012)	Steers	3/4 Holstein × Zebu	SF_6	113.0	Cultivars of sugarcane plus urea
Fiorentini et al. (2014)	Steers	Nellore	SF_6	91.7	Lipid sources with different fatty acid profiles
Fitzsimons et al. (2013)	Heifers	Simmental	SF_6	260.0	Different residual feed intakes using 100 grass silage
Grainger et al. (2008)	Steers	Holstein	SF_6	399.0	Supplementation with whole cottonseed
Gutierrez et al. (2007)	Steers	Holstein	SF_6	113.8	Concentrations of nitroethane plus dry rolled corn
Hales et al. (2012)	Steers	Jersey	Chambers	38.8	Different corn processing methods plus inclusion of WDGS
Hales et al. (2013)	Steers	Jersey	Chambers	46.1	Increments of WDGS in steam flaked corn based diets
Hales et al. (2014a)	Steers	Cross	Portable head boxes	93.3	Levels of dietary roughage using dry rolled corn and WDGS diets
Hales et al. (2014b)	Steers	MARC 1	Portable head boxes	107.5	Levels of glycerin on energy metabolism, nutrient balance and eCH_4
Hart et al. (2009)	Heifers	Charolais cross	SF_6	138.0	Levels of sward dry matter digestibility
Henry et al. (2015)	Heifers	Crossbreed	SF_6	87.5	Effects of chitosan on nutrient digestibility
Hegarty et al. (2007)	Steers	Angus	SF_6	142.3	Greater and lower residual feed intake
Hosoda et al. (2012)	Steers	Holstein	Chambers	99.9	Levels of soy sauce cake
Hulshof et al. (2012)	Steers	Nellore × Guzera	SF_6	85.0	Effects of nitrate supplementation of sugarcane based diets
Hunerberg et al. (2013a,b)	Heifers	Crossbred	Chambers	119.0	Effects of DDGS using finishing and growing beef cattle diets
Jiao et al. (2013)	Heifers	Holstein	Chambers	96.4	Efficiency of energy using UK diets
Jones et al. (2011)	Steers	Angus	FTIR	125.1	High and low residual feed intake with low and high quality of pasture
Jordan et al. (2006a)	Steers	Charolais - Limousin	SF_6	55.4	Effects of refined soy oil and whole soybeans

		cross			
Jordan et al. (2006b)	Heifers	Charolais - Limousin cross	SF_6	55.4	Effects of refined coconut oil or copra meal
Lee et al. (2015)	Heifers	Crossbred	Chambers	183.0	Effect of source of nitrate
Li et al. (2012)	Steers	Holstein	Chambers	82.4	Sources of saponins
Lila et al. (2005)	Steers	Holstein	Chambers	77.0	Effects of sarsaponin on ruminal fermentation
Lovett et al. (2003)	Heifers	Charolais cross	SF_6	112.2	Different ratios of forage and grain with or without coconut oil
Mc Geough et al. (2010a)	Steers	Continental crossbred	SF_6	180.0	Different ratios of wheat grain and straw/chaff
Mc Geough et al. (2010 b)	Steers	Crossbred	SF_6	228.0	Stages of silage corn maturity
McGinn et al. (2004)	Steers	Holstein	Chambers	129.0	Monensin, sunflower oil, enzymes, yeast and fumaric acid
McGinn et al. (2009)	Steers	Hereford	SF_6	177.0	Effects of DDGS
Molano et al. (2006)	Steers	Hereford × friesian	SF_6	89.1	Effects of New Zealand hill pasture in different seasons
Newbold et al. (2014)	Steers	Holstein	Chambers	86.8	Effects of dietary nitrate levels
Pinares-Patiño et al. (2003)	Steers	Charolais	SF_6	204.4	Physiological stages of Timothy grass
Romero-Pérez et al. (2014)	Heifers	Angus	Chambers	203.	Use of 3-nitrooxypropanol
Romero-Pérez et al. (2015)	Heifers	Angus	Chambers	157.9	Long term use of 3-nitrooxypropanol
Stackhouse et al. (2011)	Steers	Angus	Chambers	68.4	Emissions from Holstein Angus-cross feedlot steers during representative growth stages
Stackhouse et al. (2013)	Steers	Angus	Chambers	239.0	Effects of growth promoting technologies on animal performance and emission rates
Staerfl et al. (2012)	Steers	Brown Swiss × Limousin	Chambers	37.4	Long term evaluation of feeding acacia tannin, garlic, maca and lupine to bulls fattened on grass or corn silage
Troy et al. (2015)	Steers	Charolais and	Chambers	194.3	Effects of nitrate addition and oil

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Vyas et al. (2014a)	Heifers	Crossbred	Chambers	177.5	*Propionibacterium* strains using high-forage diets
Vyas et al. (2014b)	Heifers	Crossbred	Chambers	138.5	*Propionibacterium* strains using corn grain based diets
Vyas et al. (2015)	Heifers	Crossbred	Chambers	187.8	Effects on vivo of *Propionibacterium* strains
Vyas et al. (unpublished)	Steers	Crossbred	Chambers	125.9	Use of 3-nitrooxypropanol for backgrounding and finishing cattle

Note: [1]Average for each study.

DDGS, dried distillers grains plus solubles; FTIR, Fourier transform infrared spectroscopy; IVOMD, in vitro organic matter digestibility; SF_6, sulfur hexafluoride tracer gas technique; WDGS, wet distillers grains with solubles.

Supplementary Table 2.2. Methane prediction (MJ d^{-1}) equations for beef cattle used in the study.

N	Original source	Equation	
1	IPCC (2006), Tier 2	$CH_4 =$	$(DMI \times 18.5\ (MJ\ kg^{-1}\ DM) \times Y_m)\ /55.65\ (MJ\ kg^{-1}\ CH_4)$
2	Ellis et al. (2007), 1b	$CH_4 =$	$4.38 + 0.0586 \times MEI$
3	Ellis et al. (2007), 2b	$CH_4 =$	$3.96 + 0.561 \times DMI$
4	Ellis et al. (2007), 3b	$CH_4 =$	$4.79 + 0.0492 \times \text{forage}\ (\%)$
5	Ellis et al. (2007), 4b	$CH_4 =$	$5.263 + 6.93 \times \text{lignin}$
6	Ellis et al. (2007), 5b	$CH_4 =$	$5.58 + 0.848 \times NDF$
7	Ellis et al. (2007), 6b	$CH_4 =$	$5.70 + 1.41 \times ADF$
8	Ellis et al. (2007), 7b	$CH_4 =$	$3.05 + 0.0371 \times MEI + 0.801 \times NDF$
9	Ellis et al. (2007), 8b	$CH_4 =$	$3.31 + 0.0382 \times MEI + 1.05 \times ADF$
10	Ellis et al. (2007), 9b	$CH_4 =$	$0.357 + 0.0591 \times MEI + 0.0500 \times \text{forage}\ (\%)$
11	Ellis et al. (2007), 10b	$CH_4 =$	$-1.02 + 0.681 \times DMI + 0.0481 \times \text{forage}\ (\%)$
12	Ellis et al. (2007), 11b	$CH_4 =$	$2.30 + 1.12 \times DMI - 6.26 \times \text{lignin}$
13	Ellis et al. (2007), 12b	$CH_4 =$	$2.7 + 1.16 \times DMI - 15.8 \times EE$
14	Ellis et al. (2007), 13b	$CH_4 =$	$0.183 + 0.0433 \times MEI + 0.647 \times NDF + 0.0372 \times \text{forage}\ (\%)$
15	Ellis et al. (2007), 14b	$CH_4 =$	$2.94 + 0.0585 \times MEI + 1.44 \times ADF - 4.16 \times \text{lignin}$
16	Ellis et al. (2009), A	$CH_4 =$	$2.29 + 0.670 \times DMI$
17	Ellis et al. (2009), B	$CH_4 =$	$3.05 + 3.71 \times CEL$
18	Ellis et al. (2009), C	$CH_4 =$	$4.72 + 1.13 \times \text{starch}$
19	Ellis et al. (2009), D	$CH_4 =$	$6.01 + 0.345 \times NFC$
20	Ellis et al. (2009), E	$CH_4 =$	$3.46 + 5.06 \times \text{sugar}$
21	Ellis et al. (2009), F	$CH_4 =$	$3.32 - 1.23 \times \text{starch} + 9.48 \times \text{sugar}$
22	Ellis et al. (2009), G	$CH_4 =$	$-1.01 + 2.76 \times NDF + 0.722 \times \text{starch}$
23	Ellis et al. (2009), H	$CH_4 =$	$2.26 + 5.02 \times \text{sugar} + 0.0236 \times \text{forage}\ (\%)$
24	Ellis et al. (2009), I	$CH_4 =$	$2.72 + 0.0937 \times MEI + 4.31 \times CEL - 6.49 \times HC - 7.44 \times \text{fat}$

25	Ellis et al. (2009), J	$CH_4 =$	$0.310 + 2.88 \times \text{CEL} + 4.15 \times \text{CP} - 3.97 \times \text{fat}$
26	Ellis et al. (2009), K	$CH_4 =$	$0.561 + 5.86 \times \text{CEL} + 0.526 \times \text{NFC}$
27	Ellis et al. (2009), L	$CH_4 =$	$2.61 + 0.0687 \times \text{MEI} + 5.99 \times \text{sugar} - 2.15 \times \text{starch}$
28	Ellis et al. (2009), M	$CH_4 =$	$2.79 - 1.04 \times (\text{NFC:NDF}) + 0.798 \times \text{DMI}$
29	Ellis et al. (2009), N	$CH_4 =$	$2.68 - 1.14 \times (\text{starch:NDF}) + 0.786 \times \text{DMI}$
30	Ellis et al. (2009), O	$CH_4 =$	$2.58 - 0.339 \times (\text{NFC:ADF}) + 0.774 \times \text{DMI}$
31	Ellis et al. (2009), P	$CH_4 =$	$2.50 - 0.367 \times (\text{starch:ADF}) + 0.766 \times \text{DMI}$
32	Ellis et al. (2009), Q	$CH_4 =$	$7.09 \times \{1 - \exp^{[-18.9 \times \text{fat}]}\}$
33	Ellis et al. (2009), R	$CH_4 =$	$8.53 \times \{1 - \exp^{[-0.637 \times \text{NDF}]}\}$
34	Ellis et al. (2009), S	$CH_4 =$	$8.76 \times \{1 - \exp^{[-1.86 \times \text{HC}]}\}$
35	Ellis et al. (2009), T	$CH_4 =$	$8.51 \times \{1 - \exp^{[-5.50 \times \text{lignin}]}\}$
36	Ellis et al. (2009), U	$CH_4 =$	$8.23 \times \{1 - \exp^{[-1.68 \times \text{ADF}]}\}$
37	Ellis et al. (2009), V	$CH_4 =$	$8.48 \times \{1 - \exp^{[-0.0230 \times \text{MEI}]}\}$
38	Ellis et al. (2009), W	$CH_4 =$	$10.8 \times \{1 - \exp^{[-0.141 \times \text{DMI}]}\}$
39	Ellis et al. (2009), W1	$CH_4 =$	$10.8 \times (1 - \exp^{\{-[-0.0127 \times (\text{NFC: ADF}) + 0.220] \times \text{DMI}\}})$
40	Ellis et al. (2009), W2	$CH_4 =$	$10.8 \times (1 - \exp^{\{-[-0.0138 \times (\text{starch:ADF}) + 0.211] \times \text{DMI}\}})$
41	Ellis et al. (2009), W3	$CH_4 =$	$10.8 \times (1 - \exp^{\{-[-0.034 \times (\text{NFC: NDF}) + 0.228] \times \text{DMI}\}})$
42	Yan et al. (2009), iib	$CH_4 =$	$[[32.4 - 305.8\ \text{ME/GE} + 199.1\ \text{DE/GE} + 4.4\ \text{ME}]\ \text{DMI} - 14.9] \times 0.66] \times 0.0556$
43	Yan et al. (2009), iiib	$CH_4 =$	$[[1.749 - 12.18\ \text{ME/GE} + 10.74\ \text{DE/GE}]\ \text{GEI} - 14.0] \times 0.66] \times 0.0556$
44	Ricci et al. (2013), GEI	$CH_4 =$	$74.34 + 0.57 \times \text{GEI} - 10.61 \times \text{feed} - 69.67 \times \text{stage} - 0.22 \times \text{GEI} \times \text{feed} + 0.57 \times \text{GEI} \times \text{stage}$
45	Ricci et al. (2013), DMI	$CH_4 =$	$9.87 + 9.95 \times \text{DMI} - 15.15 \times \text{feed} - 74.48 \times \text{stage} - 3.67 \times \text{DMI} \times \text{feed} + 10.90 \times \text{DMI} \times \text{stage}$
46	Moraes et al. (2014), H-GEL	$CH_4 =$	$1.289 + 0.051 \times \text{GEI}$
47	Moraes et al. (2014), H-DL	$CH_4 =$	$-0.163 + 0.051 \times \text{GEI} + 0.038 \times \text{NDF}\ (\%)$
48	Moraes et al. (2014), H-AL	$CH_4 =$	$-1.487 + 0.046 \times \text{GEI} + 0.032 \times \text{NDF}\ (\%) + 0.006 \times \text{BW}$
49	Moraes et al. (2014), S-GEL	$CH_4 =$	$0.743 + 0.054 \times \text{GEI}$
50	Moraes et al. (2014), S-DL	$CH_4 =$	$0.743 + 0.054 \times \text{GEI}$
51	Moraes et al. (2014), S-AL	$CH_4 =$	$-0.221 + 0.048 \times \text{GEI} + 0.005 \times \text{BW}$

Note: ADF, acid detergent fiber (kg d^{-1}); AL, animal level; BW, body weight (kg); CEL, cellulose (kg d^{-1}); CP, crude protein (kg d^{-1}); DE, digestible energy (MJ kg^{-1} DM); DL, dietary level; DMI, dry matter intake (kg d^{-1}); GE, gross energy (MJ kg^{-1} DM); GEI, gross energy intake (MJ d^{-1}); GEL, gross energy level; H, heifers; HC, hemicellulose (kg d^{-1}); ME, metabolizable energy (MJ kg^{-1} DM); MEI, metabolizable energy intake (MJ d^{-1}); NDF, neutral detergent fiber (kg d^{-1}); NFC, non-fiber carbohydrate (kg d^{-1}); NSC, non-structural carbohydrates (kg d^{-1}); S, steers; stage, physiological stage (nonlactating or lactating); Y_m, Methane conversion factor (6.5 for diets greater than 90 g forage kg^{-1} DM, 3 for diets equal to or less than 90 g forage kg^{-1} DM).

Supplementary Table 2.3. Methane prediction (MJ d^{-1}) equations for beef cattle ordered according to combined index for the high-forage dataset.

Equation	R^2 adjusted	r_c	C_b	RMSPE (g d^{-1})	ECT %	ER %	ED %	MEF	CD	CI	Ranking
IPCC 2006	0.577	0.715	0.95	39.81	1.23	0.03	98.74	0.56	1.81	24	1
Moraes et al. (2014) S-AL	0.632	0.725	0.90	42.85	8.90	3.93	87.17	0.59	2.17	39	2
Moraes et al. (2014) S-SIM AL	0.572	0.646	0.87	45.87	1.77	3.14	94.54	0.52	2.53	44	3
Moraes et al. (2014) S-GEL	0.425	0.678	0.86	45.76	12.80	5.44	81.76	0.53	2.45	53	4
Ellis et al. (2009) - N	0.589	0.601	0.77	35.58	9.31	14.30	76.38	0.47	3.31	56	5
Moraes et al. (2014) S-DL	0.617	0.678	0.86	45.76	12.80	5.44	81.76	0.53	2.45	57	6
Moraes et al. (2014) H-AL	0.585	0.568	0.84	30.60	14.87	0.50	84.63	0.36	2.08	60	7
Moraes et al. (2014) H-SIM DL	0.522	0.643	0.84	29.30	27.79	0.91	71.30	0.41	1.56	61	8
Moraes et al. (2014) S-SIM GEL	0.597	0.600	0.84	48.70	3.59	3.72	92.16	0.46	2.87	63	9
Yan et al. (2009) (iiib)	0.554	0.816	0.91	37.31	46.64	1.61	52.10	0.61	0.89	63	10
Ellis et al. (2007) - 14b	0.513	0.568	0.81	47.00	0.34	7.07	92.60	0.45	3.86	64	11
Ellis et al. (2009) - P	0.401	0.550	0.76	37.30	6.54	10.23	83.23	0.42	3.70	65	12
Moraes et al. (2014) S-SIM DL	0.521	0.600	0.84	48.70	3.59	3.72	92.16	0.46	2.87	67	13
Ellis et al. (2009) - M	0.803	0.574	0.75	37.16	14.06	12.12	73.82	0.43	3.03	70	14
Ellis et al. (2009) - G	0.391	0.558	0.90	40.35	7.58	0.52	91.90	0.32	1.95	72	15
Ellis et al. (2009) - O	0.588	0.533	0.76	38.38	8.36	7.01	84.63	0.39	3.41	74	16
Yan et al. (2009) (iib)	0.522	0.783	0.90	41.72	45.84	4.44	50.06	0.51	0.80	81	17
Moraes et al. (2014) H-SIM AL	0.761	0.636	0.89	27.96	7.87	0.80	91.33	-2.02	0.15	83	18
Ellis et al. (2009) - B	0.472	0.453	0.82	41.98	4.52	0.01	95.47	0.27	3.04	87	19
Ellis et al. (2007) - 11b	0.319	0.534	0.87	50.45	1.06	0.17	98.78	0.37	2.89	89	20
Moraes et al. (2014) H-SIM GEL	0.756	0.639	0.80	31.12	43.96	0.56	55.48	0.34	1.20	90	21
Yan et al. (2009) SIM - (iiib)	0.538	0.738	0.87	44.09	49.74	0.39	50.20	0.46	0.93	90	22
Ellis et al. (2007) - 1b	0.643	0.523	0.71	47.61	0.05	19.00	80.96	0.44	5.85	94	23
Ellis et al. (2007) - 9b	0.602	0.520	0.75	49.22	4.03	8.38	87.59	0.40	4.14	95	24
Ellis et al. (2007) - 7b	0.406	0.553	0.70	47.22	7.48	22.67	69.85	0.45	4.39	97	25
Ellis et al. (2009) - J	0.469	0.566	0.90	42.84	16.04	3.23	80.73	0.24	1.36	97	26
Moraes et al. (2014) H -DL	0.486	0.556	0.78	33.40	35.25	0.27	64.48	0.24	1.40	101	27
Ellis et al. (2009) - W1	0.746	0.370	0.57	41.01	0.51	16.98	82.51	0.30	9.97	105	28

Ellis et al. (2007) - 13b	0.491	0.543	0.74	49.22	12.30	10.94	76.75	0.40	3.29	108	29
Yan et al. (2009) SIM - (iib)	0.563	0.716	0.85	46.75	53.12	0.73	46.47	0.39	0.86	109	30

Note: AL, animal level; DL, dietary level; GE, gross energy (MJ kg^{-1} DM); GEI, gross energy intake (MJ d^{-1}); GEL, gross energy level; H, heifers; S, steers; SIM, calculated.

Supplementary Table 2.4. Methane prediction (MJ d^{-1}) equations for beef cattle ordered according to combined index for the high-grain dataset.

Equation	R^2 adjusted	r_c	C_b	RMSPE (g d^{-1})	ECT %	ER %	ED %	MEF	CD	CI	Ranking
Ellis et al. (2009) - I	0.163	0.445	0.84	62.87	2.32	0.16	97.52	0.26	3.00	24	1
Ricci et al. (2013) - GEI	0.235	0.354	0.93	47.43	3.61	0.11	96.29	0.25	8.08	24	2
Moraes et al. (2014) S-GEL	0.294	0.406	0.71	56.35	6.02	2.67	91.31	0.27	1.68	26	3
Moraes et al. (2014) S-DL	0.294	0.406	0.71	56.35	6.02	2.67	91.31	0.27	1.68	30	4
Moraes et al. (2014) S-AL	0.204	0.376	0.66	57.41	7.78	3.99	88.23	0.24	5.18	37	5
Moraes et al. (2014) S-SIM GEL	0.625	0.521	0.67	53.88	3.41	27.83	72.52	0.44	2.20	37	6
Ellis et al. (2009) - A	0.216	0.278	0.56	65.21	0.72	4.15	95.13	0.20	9.74	44	7
Ellis et al. (2007) - 9b	0.253	0.341	0.61	64.92	9.84	4.07	86.10	0.20	4.56	47	8
Moraes et al. (2014) S-SIM DL	0.610	0.481	0.60	55.51	3.21	32.78	61.84	0.44	2.20	48	9
Ellis et al. (2007) - 8b	0.185	0.253	0.51	65.08	0.59	5.95	93.46	0.19	12.34	49	10
Ellis et al. (2007) - 7b	0.133	0.232	0.52	66.07	0.42	3.12	96.46	0.17	11.97	53	11
Ellis et al. (2009) - C	0.251	0.351	0.67	66.46	11.26	1.28	87.46	0.17	3.67	54	12
Ellis et al. (2007) - 2b	0.171	0.218	0.49	66.25	0.29	4.25	95.46	0.16	14.26	60	13
Moraes et al. (2014) S-SIM AL	0.583	0.429	0.55	58.15	11.64	31.03	59.23	0.35	7.16	60	14
Ellis et al. (2007) - 14b	0.178	0.325	0.63	67.12	13.22	1.71	85.08	0.14	3.68	62	15
Ricci et al. (2013) - SIM GEI	0.548	0.261	0.48	66.35	5.33	9.72	84.95	0.10	11.97	68	16
Ricci et al. (2013) - DMI	0.156	0.229	0.46	67.62	5.01	6.51	88.47	0.07	12.72	73	17
Ellis et al. (2009) - W	0.262	0.203	0.38	68.11	5.37	12.52	82.11	0.13	11.22	81	18
Ellis et al. (2009) - P	0.049	0.244	0.64	75.29	19.21	0.36	80.43	-0.06	2.49	88	19
Moraes et al. (2014) H-DL	0.752	0.649	0.72	32.79	59.26	27.87	12.87	-0.50	0.31	92	20
Ellis et al. (2007) - 1b	0.288	0.287	0.51	74.16	31.33	3.24	65.44	-0.05	2.13	94	21
Ellis et al. (2009) - O	0.052	0.252	0.65	76.14	21.03	0.63	78.34	-0.08	2.23	96	22
Ellis et al. (2009) - D	0.321	0.143	0.24	68.84	2.10	23.95	73.95	0.11	28.96	97	23
Ellis et al. (2009) - V	0.338	0.119	0.20	69.78	2.64	27.20	70.16	0.09	28.86	106	24
Ellis et al. (2009) - W2	-0.012	0.196	0.64	78.08	18.38	2.06	79.56	-0.14	2.39	106	25
Ellis et al. (2009) - W1	-0.003	0.219	0.69	78.34	18.66	3.06	78.28	-0.15	2.13	107	26
Moraes et al. (2014) H-GEL	0.809	0.544	0.60	43.99	66.75	26.97	6.29	-1.70	0.20	109	27

Ellis et al. (2007) - 11b	0.155	0.278	0.60	78.96	34.11	0.05	65.84	-0.19	1.55	110	28
Ellis et al. (2009) - Q	0.066	0.028	0.09	75.93	9.92	6.52	83.56	-0.08	9.14	110	29
Ellis et al. (2007) - 13b	0.128	0.208	0.44	76.45	27.95	2.49	69.56	-0.11	2.46	112	30

Note: AL, animal level; DL, dietary level; GE, gross energy (MJ kg^{-1} DM); GEI, gross energy intake (MJ d^{-1}); GEL, gross energy level; H, heifers; S, steers; SIM, calculated.

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CHAPTER 3. Universally applicable methane prediction equations for beef cattle fed high- or low forage diets[2].

3.1. Introduction

Methane is a greenhouse gas and livestock farming is a major contributor to atmospheric methane mainly emitted by enteric fermentation from livestock operations. Beef production contributes 41 percent of global livestock emissions (Gerber et al. 2013).

Models that predict CH_4 emissions from ruminants are used to estimate emission inventories, develop mitigation options and implement policies. Numerous mechanistic, dynamic or mathematical models have been developed and recommended for prediction of CH_4 for all kinds of cattle. Empirical models specifically for beef cattle (e.g., Ellis et al. 2007, 2009; Yan et al. 2009; Muir et al. 2011 and Moraes et al. 2014) or for beef and dairy cattle (e.g., Ricci et al. 2013; Ellis et al. 2014) or for beef, dairy and sheep (Ramin and Huhtanen 2013) have been proposed. However, the uncertainty of estimates of CH_4 from beef cattle using these models can be substantial (Hippenstiel et al. 2013; Moraes et al. 2014), especially for cattle fed high-grain diets (Escobar-Bahamondes et al. 2016). Part of this uncertainty could be due to the limitations of the model, but variability can also be due to limited records, regional representation of data, and statistical distribution or range of each variable within the development database. Application of models outside the

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[2] A version of this chapter has been published. Escobar-Bahamondes, P., Oba, M. and Beauchemin, K. A. 2016. Universally applicable methane prediction equations for beef cattle fed high- or low forage diets. Canadian Journal of Animal Science (in press).

production systems upon which they were developed can lead to errors in greenhouse gas estimates (Schils et al. 2013).

The Intergovernmental Panel on Climate Change (IPCC 2006) established several methodologies (Tiers) to estimate CH_4 emissions from cattle. Tier 1 uses a yearly emission factor ranging from 47 to 56 kg of CH_4 depending upon the geographical zone, which is multiplied by the number of cattle. Tier 2 uses an Y_m based on daily GEI (MJ d^{-1}). The Y_m for diets containing 90% or more concentrate (feedlot cattle) is 3% ± 1% of GEI, whereas Y_m is 6.5% ± 1% for all other diets and cattle categories. Tier 3 is recommended for estimating CH_4 emissions for those countries where livestock emissions are particularly important and where there are data on animal numbers and feed composition.

In most beef cattle production systems, cattle are fed diets high in forage (e.g., 80% forage, 20% grain) with the exception of feedlots, which finish cattle on high-grain diets (e.g., 20% forage, 80% grain). The effect of diet composition on CH_4 in beef cattle has been reviewed extensively by Beauchemin and McGinn (2005) and Doreau et al. (2011). Fernando et al. (2010) reported that a major change in the ruminal microbial population structure occurred when forage content of the diet was lowered from 60% to 40% of DM, with an even more pronounced change occurring with a further shift to 20%. Additionally, differences in diet composition used in various beef production systems may not be adequately considered in current CH_4 models. It is well known that dietary forage:concentrate **(F:C)** proportion alters the rumen microbiome and resulting fermentation pattern. Diets rich in grain increase ruminal propionate proportion and decrease ruminal acetate proportion, a fermentation pattern associated with less CH_4 (Beauchemin et al. 2009). Furthermore, some models require inputs that are not easily available (e.g., values of digestibility, ME or DE), limiting their practical use.

We hypothesized that developing equations specific for high-forage (≥ 40% forage DM; **HF**) and low forage (≤ 20% forage DM; **LF**) diets using a universal database would improve the prediction of CH_4 emissions from beef cattle compared with the non diet-specific Tier 2 equation of IPCC. The aims of this study were to: 1) construct a database of CH_4 emissions for beef cattle fed forage and grain based diets from published literature worldwide, 2) develop a set of practical equations to predict production of enteric CH_4 that could be used universally, and 3) compare predictions using these new equations with those of IPCC (2006) Tier 2.

3.2. Materials and methods

3.2.1. Datasets

The original database was constructed using peer-reviewed scientific papers published between 2000 and 2014 that reported effects of diets on CH_4 for beef cattle. The Web of Science (Thomson Reuters, New York, USA) and Papers© v2.6.4 (Mekentosj B.V., Dordrecht, The Netherlands) were used to search for relevant peer-reviewed publications. Keywords used were: “methane”, “methane in steers and heifers”, and “methane in beef cows”. Published papers were included in the database if they provided a description of the diets and results for CH_4. Initially, the database considered 58 studies, representing 197 treatments means for CH_4 from beef cattle. Each treatment (record) contained information on animal characteristics (breed, sex and BW), treatment general description, dietary ingredients and chemical composition, DMI, and CH_4. Criteria for selecting data to include in the database were: measured CH_4, DMI and dietary chemical composition. Treatment means for additives that significantly inhibited CH_4 were removed from the database. If studies did not report the full chemical composition of diets, the values were estimated from feed tables, using data provided within the paper, or by diet formulation software (CPM-Dairy®, University of Pennsylvania, Philadelphia, USA; Rumnut©, Chalcombe, Southampton, UK; BCNRM® beef cattle model [National Academies of Sciences, Engineering, and Medicine 2016]) or using international websites such as The National Animal Nutrition Program for America and Canada ([Online] Available: http://nanp-nrsp-9.org [2016 Feb. 01]) and Feedipedia for Europe ([Online] Available: www.feedipedia.org [2016 Feb. 01]) that provide feed databases with exhaustive descriptions of chemical composition of individual feeds.

To reflect differences in ruminal microbial populations due to diet (Fernando et al. 2010), proportion of dietary forage was used as a criterion to divide the database into two datasets. One dataset comprised data from treatment with greater than or equal to 40% dietary forage (40 to 100%; n = 148 from 38 studies), representing HF diets fed to breeding stock and growing animals. The other dataset comprised treatments with 20% or less dietary forage (2 to 14%; n = 43 from 17 studies), representing LF diets fed to feedlot finishing cattle. Treatments with less than 40% but greater than 20% forage were considered as transition diets and excluded due to their small numbers (n=6; 3 studies). The dietary variables included in both datasets are presented in supplementary Table 3.1 where production of CH_4 (g d^{-1}) was the response variable.

Mahalanobis distance was used to detect and exclude outliers (Kleinbaum et al. 1988). Collinearities between variables were evaluated by variance inflation factors between CH_4 and dietary composition and intakes. Collinearity was identified when variance inflation was ≥ 10, in which case the variable with the lowest *r* in predicting CH_4 was removed (Kleinbaum et al. 1988).

Two statistical methods, Monte Carlo (**MC**) methods and cluster analysis with bootstrapping were used to overcome the limited numbers of records in each dataset, as described below.

3.2.2. Monte Carlo datasets

Monte Carlo methods are algorithms that use pseudo random numbers to determine the properties of some function. Pseudo random numbers represent independent observations from a uniform distribution of data and accuracy of the method generally improves with increasing number of pseudo random numbers used (Upton and Cook 2006). To preserve collinearity between variables, each study in each original dataset was defined as a “seed” limited by a maximum and minimum value for each variable and pseudo random numbers were generated for each seed and aggregated to form the MC-HF dataset (n = 123,000) and MC-LF dataset (n = 32,000).

Table 3.1. Summary of nutrient profiles and CH_4 emissions for the original high- and low forage datasets.

	High-forage dataset ≥ 40% dietary forage (n=123)					
Variable[a]	Mean	SD[b]	Min	Max	Skewness	Kurtosis
BW (kg)	382	215.4	107	666	-0.03	-0.06
Forage proportion (% DM)	71.9	32.63	40.0	100.0	0.34	-0.84
DMI (kg d^{-1})	7.4	3.55	3.5	12.0	0.17	-0.28
Forage intake (kg DM d^{-1})	5.2	3.32	1.8	10.7	0.63	0.69
CP (% DM)	15.1	6.59	5.9	29.0	1.31	2.77
NDF (% DM)	38.9	16.44	21.6	68.8	1.15	2.02
ADF (% DM)	23.5	11.93	11.9	43.2	1.11	0.89
NFC[c] (% DM)	36.9	19.75	7.9	63.5	-0.26	0.23
HC (% DM)	15.2	8.78	5.2	31.3	0.65	0.55
CEL (% DM)	19.8	10.50	10.0	34.6	0.99	0.37
Fat (% DM)	3.7	2.41	0.9	8.2	1.15	2.30
Sugar (% DM)	6.3	5.22	2.1	16.1	0.57	0.12
Starch (% DM)	21.2	25.15	0.3	53.6	0.13	-0.81
GE (MJ kg^{-1} DM)	18.4	2.29	14.0	20.9	-3.43	5.44
ME (MJ kg^{-1} DM)	9.9	2.72	5.4	13.3	0.01	-0.44
Methane (g d^{-1})	154.1	113.19	37.4	322.0	0.96	0.90
	Low forage dataset ≤ 20% dietary forage (n=34)					
BW (kg)	447	199.5	300	589	-0.09	-1.66
Forage proportion (% DM)	9.5	3.79	2.0	14.0	-1.69	7.70
DMI (kg d^{-1})	8.5	4.73	5.4	14.1	2.37	8.46
Forage intake (kg DM d^{-1})	0.8	0.58	0.2	1.4	1.36	4.96
CP (% DM)	15.7	6.89	11.9	23.1	0.83	-0.63
NDF (% DM)	17.3	8.04	11.6	27.9	0.84	0.31
ADF (% DM)	8.3	4.97	3.5	16.5	1.45	1.67
NFC (% DM)	57.7	17.75	41.5	70.0	-0.50	-0.72
HC (% DM)	9.0	5.69	2.2	17.7	0.36	-0.07
CEL (% DM)	6.5	4.86	2.4	15.1	1.67	2.35
Fat (% DM)	4.4	4.48	1.5	11.0	1.12	2.37
Sugar (% DM)	4.7	1.89	2.7	6.6	0.24	-0.89
Starch (% DM)	48.1	18.09	31.9	61.7	-0.09	-1.19
GE (MJ kg^{-1} DM)	18.4	3.10	14.2	25.1	1.46	9.16
ME (MJ kg^{-1} DM)	12.5	2.49	10.1	15.4	-0.07	-0.75
Methane (g d^{-1})	108.0	78.5	46.1	190.2	1.29	4.25

Note: [a]ADF, acid detergent fiber; BW, body weight; CEL, cellulose; CP, crude protein; DM, dry matter; DMI, dry matter intake; GE, gross energy; HC, hemicellulose; ME, metabolizable energy; NDF, neutral detergent fiber; NFC, non-fiber carbohydrate.

[b]SD, standard deviation.

[c]Most studies in the database did not report NFC, HC, CEL sugar or ME of diets hence these values were mostly estimated.

3.2.3 Cluster (Bootstrap) datasets

Cluster analysis is a multivariate technique of classification based on grouping data that share similar values from any number of variables (SAS Institute 2015). The aim of classification is to group treatments based on their variables, such that treatments within a group are more similar than treatments within other groups. Bootstrapping and randomization techniques have been in use in diverse fields of biology (Manly 2007) and in animal science in recent years (McMeniman et al. 2010; Marcondes et al. 2015). Thus, the original HF dataset was divided into four clusters and the original LF dataset was divided into three clusters using K-means cluster technique (SAS Institute 2013). Each cluster was resampled 1,000 times using a bootstrapping (**BT**) technique with replacement to create new BT-HF (n = 123,000) and BT-LF (n = 32,000) datasets.

3.2.4. Regression analyses

A modification of the approach used by Marcondes et al. (2012) was implemented to develop new prediction equations. Initially, principal component analysis (**PCA**) was separately conducted for each original database (HF and LF) to identify independent variables that were most related to CH_4. Principal component analysis is a multivariate technique that reduces the dimensionality of data by transforming related variables into a set of uncorrelated variables retaining as much variation as possible (Abdi and Williams 2010). Variables selected from PCA were used as input variables to build the models. Polynomial variables were included in the various new models. Multicollinearity between linear and polynomial regressors was identified by variance inflation factors where variables with values > 10 were removed. Using the original database, and HF and LF datasets, forward stepwise regressions were performed to obtain equations that only included significant ($P < 0.05$) variables. Initially, equations were selected based on RMSE and Akaike's Information Criterion corrected. The MIXED procedure was used to include study as a random effect to account for differences among studies (St-Pierre 2001). An internal validation of the original equations developed was achieved using "leave-one-out" cross validation (Arlot and Celisse 2010). The MC and bootstrapping datasets were used to develop equations by applying forward stepwise regression and internal validation was achieved by K-fold cross validation (n = 10). Non-significant variables ($P > 0.05$) were manually excluded and final equations were selected based on RMSE and K-fold R^2. Statistical analysis was performed using JMP© v12.0 (SAS Institute Inc., Cary, NC, USA) and XLSTAT© (Addinsoft, Paris, France).

3.2.5. Equation performance

Observed minus predicted values were used to evaluate performance of equations using r_c, RMSPE, mean absolute error (**MAE**), MEF, and index of agreement (***dr***) of the equations. Statistics were computed in accordance with Tedeschi (2006) and Willmott et al. (2011). The RMSPE was calculated from MSPE. The MSPE was split into: ECT (%) to assess whether the model over- or under predicted CH_4; ER (%) representing error attributable to regression; and ED (%) that provides an indication of the adequacy of the model for prediction (Bibby and Toutenburg 1977). If the majority of the error is due to ED, the model is considered to have no systematic errors and to be adequate for prediction. It is assumed that greater values for r_c (≤ 1.0), MEF (≤1.0), and ED (≤100%), smaller values of RMSPE, ECT, ER, and MAE, and values for *dr* equal to 0, represent a better-fit equation. Residual analysis was made by regressing the centered predicted values of CH_4 against the observed minus predicted values as was suggested by St-Pierre (2003).

3.2.6. IPCC 2006 equation

Prediction of CH_4 using Tier 2 methodology (IPCC 2006) was calculated as follows: CH_4 (g d^{-1}) = DMI (kg d^{-1}) × 18.5 (MJ kg^{-1} DM) × Y_m) / 55.65 (MJ kg^{-1} CH_4), where Y_m = 3.0% when dietary concentrate proportion is ≥ 90%, else Y_m = 6.5%.

3.3 Results and discussion

The complete database that was comprised of dietary composition, daily intakes and animal data was split into two parts: HF (≥ 40% dietary forage content) and LF (≤ 20% dietary forage content) diets based on the knowledge that cattle fed HF diets produce more CH_4 than cattle fed grain-based diets (Rooke et al. 2014). McCann et al. (2014) and Fernando et al. (2010) indicated that dietary F:C produces marked changes in the ruminal bacterial community when diets shift from a F:C of 60:40 to 20:80. A F:C of 20:80 or less is associated with an increase of amylolytic bacterial species leading to lower CH_4. Furthermore, McCann et al. (2014) and Fernando et al. (2010) suggested that the threshold F:C of 10:90 used by IPCC (2006) may be too low, and thus the definition of LF diets in the present study was expanded to incorporate diets up to a F:C of 20:80.

3.3.1 Datasets and relationships between methane production and dietary or animal variables.

Summary descriptions of the datasets are presented in Table 3.1. An important aspect of model development is that the predictive scope of a model is related to the database used in its development. Consequently, models have difficulty in predicting values of CH_4 outside the range of the dataset used. Thus, to develop widely applicable equations, the database used in our study included data from a range of diets compositions used in beef cattle production from numerous geographical locations. The accuracy and precision of the new models was compared to the widely used IPCC (2006) Tier 2 equation, but not to other extant diet-specific prediction equations as these were not meant to be applied outside the range (maximun and minimum values) of the databases used. Performance of extant prediction equations is presented by Escobar-Bahamondes et al. (2016).

Variables within a dataset often show asymmetry (Skewness) and peakedness distribution (Kurtosis) even when data are obtained from studies with normal distribution. Shape of the distribution of each variable in the database and the location of the average within the range of values can be a source of bias and limit prediction of CH_4. With the exception of Ellis et al. (2007; 2009), most studies do not report skewness and kurtosis and it is only possible to infer the distribution of variables within most previously published databases by comparing the average against the range of each dietary content variable.

Total CH_4 production is positively associated with DMI (Johnson and Johnson 1995; Shibata et al. 2010) because it is related to the quantity of organic matter fermented in the rumen (Knapp et al. 2014). As a consequence, a strong linear relationship between CH_4 and DMI was reported for beef cattle fed only forages (Charmley et al. 2016). However, feeding concentrates can affect the relationship between CH_4 and DMI, because DMI is positively associated with concentrate proportion yet CH_4 decreases with increased concentrate feeding. Furthermore, CH_4 expressed as a proportion of DMI or energy intake usually decreases with increasing DMI (Shibata et al. 2010). This is because DMI is inversely associated with ruminal digestibility of nutrients (due to increased passage rate and decreased extent of ruminal fermentation). For this reason, equations in our study predicted CH_4 (g d^{-1}) rather than CH_4 yield (g CH_4 kg^{-1} DMI). In the current study, DMI was less for the HF than the LF dataset, principally due to the lower BW of animals fed HF diets (Table 3.1).

An average forage proportion of 71.9 and 9.5% of dietary DM characterized the HF and LF datasets, respectively, with positive skewness (0.37) and platykurtic (-0.78) distribution for the HF database, and conversely negative skewness (-1.69) and leptokurtic (7.71) distribution of forage proportion in the LF database (Table 3.1). Consequently, these distributions affected the distribution of all other dietary components. Forage proportion of the HF dataset was close to mean values reported for beef cattle databases used by Ellis et al. (2007; mean 79.0%; range 9.0 to 100%), Yan et al. (2009; mean 81.9%; range 29.5 to 100%), Ricci et al. (2013; mean 79.5%; range 9.0 to 100%) and Ramin and Huthanen (2013; mean 83.0%; range 30 to 100%). Only Ellis et al. (2009; 53.7%; range 29.5 to 75%) reported a lower mean forage proportion than our HF dataset. However, the range of forage contents in those studies was greater than in our HF dataset indicating that the equations developed by them were not specific to HF diets.

The rationale for developing separate predictions for the HF and LF databases was to reflect differences in their fermentation characteristics. The HF database represents mainly cellulolytic ruminal fermentation. Fermentation of fiber yields greater proportions of acetate and butyrate than propionate. Acetate and butyrate production release hydrogen to the ruminal pool, which the methanogens use to reduce CO_2 to CH_4. Therefore, an increase in acetate:propionate ratio increases CH_4 (Johnson and Johnson, 1995). As was expected, daily intakes of NDF (2.8 vs. 1.5 kg d^{-1}) were greater in the HF vs. LF dataset. The daily mean intake of NDF (kg d^{-1}) for the HF database is similar to that of Ramin and Huthanen (2013; 2.8 kg d^{-1}), smaller than that of Ricci et al. (2013; 4.8 kg d^{-1}), Yan et al. (2009; 3.3 kg d^{-1}) and Ellis et al. (2007; 3.8 kg d^{-1}), but greater than that of Moraes et al. (2014; heifers 2.2 kg d^{-1} and steers 1.8 kg d^{-1}) and Ellis et al. (2009; 2.2 kg d^{-1}).

As expected, the proportion of NFC was smaller for the HF vs. LF dataset (36.9 vs. 57.7%). Intake of NFC (2.8 vs. 4.9 kg d^{-1}) was smaller for the HF vs. LF dataset and only the HF dataset is similar to the value reported by Ellis et al. (2009; 2.9 kg d^{-1}). Many studies in the database did not report sugar and starch contents of diets, hence these values were mostly estimated. Intake of starch was smaller for the HF vs. LF dataset (1.6 vs. 4.1 kg d^{-1}). The intake reported by Ellis et al. (2009) was 2.2 kg d^{-1}, while the other beef datasets did not report starch and sugar contents. Low forage diets with greater intakes of NFC such as sugar and starch are characterized by greater production of propionate, which is a sink for hydrogen in the rumen. High rates of fermentation of NFC produce rapid accumulation of volatile fatty acids, production of lactic acid and low ruminal pH that can inhibit growth of cellulolytic bacteria in the rumen (Hook et al. 2010). Low ruminal pH also reduces protozoal numbers thereby eliminating habitats for methanogens. With these changes in the ruminal environment, CH_4 is characteristically less in cattle fed LF than HF diets (Cottle et al. 2011).

The range of CH_4 in the HF database overlapped with the CH_4 range for the LF database. Average CH_4 for the HF and LF datasets was 154.1 and 108.0 g d^{-1} (8.6 and 6.0 MJ d^{-1}), respectively. These CH_4 values are less than the values reported by Ellis et al. (2007; 164.2 g d^{-1}, 9.1 MJ d^{-1}), Yan et al. (2009; 181.7 g d^{-1}, 10.1 MJ d^{-1}) and Ricci et al. (2013; 216.2 g d^{-1}, 12.0 MJ d^{-1}). Values of CH_4 reported by Ellis et al. (2009; 124.2 g d^{-1}, 6.9 MJ d^{-1}), Ramin and Huthanen (2014; 144.1 g d^{-1}, 8.0 MJ d^{-1}) and Moraes et al. (2014; heifers: 119.6 g d^{-1}, 6.7 MJ d^{-1}) are less than the mean CH_4 value for the HF dataset and greater than the value for the LF dataset. Values of CH_4 production from Moraes et al. (2014; steers: 108.9 g d^{-1}; 6.1 MJ d^{-1}) are similar to those of the LF dataset.

3.3.2. Relationships between methane production and animal or diet.

For the HF dataset, PCA revealed that dietary proportion variables (e.g., % of DM) were unrelated to CH_4 and thus they were not included in the CH_4 prediction equations. In contrast, BW and variables of dietary intakes were related to CH_4.

Moe and Tyrrell (1979) considered variables related to cell wall carbohydrates (HC and CEL) and cell contents (NFC and starch) to be good predictors of CH_4.

However, in our study starch had a weak relationship (*r*=0.23) with CH_4 for the HF database even though there was an extensive range in starch intakes across studies (0.02 to 3.96 kg d^{-1}). These results indicate that for HF diets variables other than starch are more important predictors of CH_4.

For the HF dataset, the variables DMI and intake of forage were more strongly correlated ($r \geq 0.70$) with CH_4 than were intakes of CP, NDF, ADF, HC, CEL, and GEI ($r < 0.70$ and ≥ 0.50; Table 3.2a). Intakes of NFC, fat, sugar and starch had moderate to weak relationships with CH_4 ($r \leq 0.5$). Correlation coefficients revealed the dietary variables (kg d^{-1}) with stronger association with CH_4 could have potential collinearity between them. For the HF dataset, DMI (kg d^{-1}) was highly correlated (*r*) with some intake variables (kg d^{-1}) including forage intake (0.74), CP (0.71), NDF (0.73), NFC (0.74) and HC (0.69).

The correlation coefficients for the LF database are reported in Table 3.2b. Similarly to the HF dataset, PCA revealed that dietary proportion variables were not related to CH_4 and they were excluded with exception of GE (MJ kg^{-1} DM) that showed a negative loading in the PCA indicating a negative correlation with CH_4. Variables related to CH_4 were BW (kg) and dietary intakes (kg d^{-1}). However, PCA found that relationships between CH_4 and CEL (kg d^{-1}) was weak (*r*=0.40), because these LF diets contain small quantities of cell wall components. In contrast to Beauchemin et al. (2009) and Patra (2013), fat (kg d^{-1}) was not related to CH_4 for the LF dataset. The lack of relationship between fat and CH_4 was probably due to the inconsistent response in CH_4 to fat across studies and a lack of treatments with high intakes of fat (> 0.5 kg d^{-1}). Intakes of cell wall components (kg d^{-1}) were highly correlated (*r*): NDF and ADF (0.90), NDF and HC (0.93), NDF and CEL (0.75), and ADF and CEL (0.94).

Table 3.2. Correlation coefficients (*r*) for relationships between animal and dietary variables for high- and low forage datasets.

a) High-forage dataset

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	BW (kg)	1.00												
2	DMI (kg d^{-1})	0.39	1.00											
3	Forage intake (kg DM d^{-1})	0.26	0.74	1.00										
4	CP (kg d^{-1})	0.16	0.71	0.68	1.00									
5	NDF (kg d^{-1})	0.31	0.73	0.81	0.54	1.00								
6	ADF (kg d^{-1})	0.32	0.61	0.78	0.47	0.91	1.00							
7	NFC (kg d^{-1})	0.35	0.74	0.26	0.32	0.16	0.06	1.00						
8	HC (kg d^{-1})	0.21	0.69	0.65	0.47	0.86	0.57	0.24	1.00					
9	Cellulose (kg d^{-1})	0.30	0.56	0.72	0.41	0.87	0.98	0.03	0.52	1.00				
10	Fat (kg d^{-1})	0.06	0.57	0.33	0.56	0.35	0.28	0.38	0.30	0.26	1.00			
11	Sugar (kg d^{-1})	-0.02	0.35	0.46	0.51	0.42	0.42	-0.07	0.34	0.40	0.26	1.00		
12	Starch (kg d^{-1})	0.32	0.55	0.01	0.11	-0.01	-0.14	0.90	0.15	-0.15	0.28	-0.38	1.00	
13	GE (MJ d^{-1})	0.34	0.98	0.69	0.73	0.68	0.53	0.74	0.69	0.48	0.61	0.34	0.56	1.00
14	Methane (g d^{-1})	0.49	0.75	0.71	0.51	0.65	0.61	0.44	0.57	0.54	0.28	0.37	0.23	0.67

b) Low forage dataset

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	BW (kg)	1.00												
2	DMI (kg d^{-1})	0.52	1.00											
3	Forage intake (kg DM d^{-1})	0.39	0.87	1.00										
4	CP (kg d^{-1})	0.23	0.68	0.50	1.00									
5	NDF (kg d^{-1})	0.43	0.81	0.69	0.81	1.00								
6	ADF (kg d^{-1})	0.40	0.71	0.61	0.79	0.90	1.00							
7	NFC (kg d^{-1})	0.50	0.84	0.71	0.35	0.51	0.49	1.00						
8	HC (kg d^{-1})	0.38	0.75	0.64	0.70	0.93	0.67	0.44	1.00					
9	Cellulose (kg d^{-1})	0.30	0.52	0.43	0.72	0.75	0.94	0.38	0.47	1.00				
10	Fat (kg d^{-1})	-0.21	-0.05	-0.11	0.25	-0.06	0.07	-0.13	-0.16	0.16	1.00			
11	Sugar (kg d^{-1})	0.46	0.82	0.73	0.82	0.77	0.78	0.50	0.64	0.64	0.04	1.00		
12	Starch (kg d^{-1})	0.46	0.80	0.70	0.23	0.38	0.33	0.96	0.37	0.21	-0.12	0.42	1.00	
13	GE (MJ d^{-1})	0.50	0.95	0.79	0.70	0.82	0.72	0.78	0.77	0.52	-0.02	0.81	0.70	1.00
14	Methane (g d^{-1})	0.81	0.79	0.64	0.54	0.70	0.61	0.61	0.66	0.40	-0.28	0.74	0.54	0.77

3.3.3. Equations to estimate methane

Cross validation was used to evaluate performance of the new equations to predict CH_4 emissions, similar to the approach used by Moraes et al. (2014). Cross validation techniques are used in nutrition research to evaluate prediction equations (e.g. Yan et al. 2009; Ramin and Huthanen 2013; Moraes et al. 2014) although it is recognized that a more robust approach would be to evaluate the equations using an independent dataset. However, that was not possible in this study due to the lack of additional independent data, especially for beef cattle fed high grain diets.

Prediction models can be of limited use for practical application if they include predictor variables that are difficult to determine by commercial feed analysis laboratories or that are not readily available. For instance, some models have used estimates of energy intake, which can be difficult to estimate under practical feeding conditions. Beef models from Yan et al. (2000) included digestible energy intake, equations from Ellis et al. (2007) and Yan et al. (2009) included ME intake, models from Ricci et al. (2013) included DM digestibility, and some models from Ramin and Huthanen (2014) used organic matter digestibility and GE digestibility. Equations developed in the current study as presented in Table 3.3 do not use digestibility, but rather rely on variables commonly reported for beef cattle feeds by commercial laboratories or values accessible from feed tables making the equations simple to implement.

Equations developed from bootstrapping datasets for HF and LF resulted in lower performance than the original dataset and the MC datasets, and therefore they are not presented and were excluded from the results and discussion.

Table 3.3. Methane prediction (g d^{-1}) equations for beef cattle developed in this study.

Dataset	ID	n		Equations[a]	CH_4 (g d^{-1})	RMSE[b]	*P*
High-forage							
Original high-forage	[HF-OR]	123	$CH_4 =$	$71.5(\pm 11.45) + 0.12(\pm 0.03) \times BW + 0.10(\pm 0.01) \times DMI^3 - 244.8(\pm 56.44) \times fat^3$	156.4	27.0	< 0.01
Monte Carlo high-forage	[HF-MC]	100,305	$CH_4 =$	$25.9(\pm 0.54) + 0.13(\pm 0.001) \times BW + 145.4 (\pm 1.31) \times fat + 10.3(\pm 0.16) \times (NDF\text{-}ADF)^2 + 0.1(\pm 0.00) \times DMI^3 - 27.4 (\pm 0.20) \times (starch:NDF)$	149.6	34.0	< 0.01
IPCC 2006 Tier 2	IPCC 2006	123	$CH_4 =$	$(DMI \times 18.5\ (MJ\ kg^{-1}\ DM) \times (6.5 \times 10))\ /55.65\ (MJ\ kg^{-1}\ CH_4)$	156.1	-	-
Low forage							
Original low forage	[LF-OR]	34	$CH_4 =$	$-26.4(\pm 20.17) + 0.21(\pm 0.04) \times BW + 30.1(\pm 11.83) \times CP - 70.5(\pm 25.48) \times fat^2 + 10.1(\pm 5.12) \times (NDF\text{-}ADF)^3$	98.3	22.2	< 0.05
Monte Carlo low forage	[LF-MC]	27,364	$CH_4 =$	$-10.1(\pm 0.62) + 0.21(\pm 0.001) \times BW + 0.36(\pm 0.003) \times DMI^2 - 69.2(\pm 1.65) \times fat^3 + 13.0(\pm 0.45) \times (CP:NDF) - 4.9(\pm 0.07) \times (starch:NDF)$	95.2	11.2	< 0.001
IPCC 2006 Tier 2	IPCC 2006	34	$CH_4 =$	$(DMI \times 18.5\ (MJ\ kg^{-1}\ DM) \times (3.0 \times 10))\ /55.65\ (MJ\ kg^{-1}\ CH_4)$	89.6	-	-
All database							
Original complete database	[AL-OR]	194	$CH_4 =$	$-35.0(\pm 17.03) + 0.08(\pm 0.03) \times BW + 1.2 (\pm 0.14) \times$ dietary forage content $- 69.8(\pm 14.4) \times fat^3 + 3.14(\pm 0.36) \times GEI$	154.9	31.9	< 0.05

Note: [a]ADF, acid detergent fiber (kg d^{-1}); BW, body weight (kg); CP, crude protein (kg d^{-1}); DMI, dry matter intake (kg d^{-1}); CH_4, enteric methane; NFC, non-fiber carbohydrate (kg d^{-1}); NDF, neutral detergent fiber (kg d^{-1}); Dietary forage content is expressed in percentage (%); Fat is expressed as kg d^{-1} and GEI is expressed as Mcal d^{-1}.

[b]RMSE, root mean square error (g d^{-1}).

3.3.4. High-forage equations

Equation [HF-OR] obtained from the original database considers BW (kg) and the polynomial variables DMI^3 (kg d^{-1}) and fat^3 (kg d^{-1}) (Table 3.3). Equation [HF-MC] considers BW (kg) and fat (kg d^{-1}) as well as $(NDF\text{-}ADF)^2$ (kg d^{-1}) and DMI^3 (kg d^{-1}) as polynomial variables, and starch:NDF. Equation [HF-OR] had a slightly smaller RMSE (27.0 g d^{-1}) than equation [HF-MC; 34.0 g d^{-1}]. However, the difference of 7.0 g d^{-1} was obtained over two datasets that substantially varied in number of records, indicating that the number of records in the HF-MC dataset was appropriate to develop models with acceptable prediction accuracy. The records used to develop equation [HF-MC] were obtained by generation of pseudo random numbers and exhaustive resampling technique producing a filled multidimensional space with major scatter of variables and CH_4 response due to the large range of dietary forage content. However, resampling techniques can lose communalities between variables, which may account for the greater RMSE of equation [HF-MC] compared with the original equation.

In equations [HF-OR] and [HF-MC], the greater estimate value for fat demonstrates its major importance in predicting CH_4, as well as its inverse relationship with CH_4 indicating its inhibitory effect on methanogenesis (Beauchemin et al. 2009; Moate et al. 2011).

3.3.5 Low forage equations

Equation [LF-OR] obtained from the original LF dataset considers BW (kg) and CP (kg d^{-1}) and polynomial effects of fat^2 and $(NDF\text{-}ADF)^3$ (Table 3.3). Equation [LF-

MC] considers BW (kg), DMI^2 (kg d^{-1}) and fat^3 (kg d^{-1}) as polynomial variables and ratios of CP:NDF and starch:NDF.

A smaller RMSE was obtained using MC [LF-MC: 11.2 g d^{-1}] compared with the original equation [LF-OR: 22.2 g d^{-1}] for the LF diets. The limited number of original records (n=34) in the LF dataset reduced the accuracy of equation [LF-OR].

3.3.6. Complete database equation

Using the complete database to develop prediction equations, resulted in equation [AL-OR] that considers BW (kg), dietary forage content (%) and polynomial effects of fat^3. The RMSE was 31.9 (g d^{-1}), which is slightly greater than the value obtained for equation [HF-OR] and lower than the value obtained for equation [HF-MC] for the HF dataset. Compared with [LF-OR] and [LF-MC], RMSE from [AL-OR] was greater indicating that non-forage specific equations are less accurate for predicting CH_4 for LF diets.

3.3.7. Performance of prediction equations

New models to predict CH_4 are generally compared with IPCC (2006) Tier 2 predictions because it is the most widely used approach for estimating CH_4 emissions from cattle. Performance comparisons of the new equations are presented in Table 3.4. Using the HF dataset, equation [HF-MC] had a greater r_c (0.813), smaller RMSPE (36.4 g d^{-1}), ECT (0.20%), MAE (27.4 g d^{-1}) and *dr* (-0.29) than IPCC (2006) and equation [HF-OR]. Equations [HF-MC] and [HF-OR] had greater MEF (0.60) than IPCC (2006). Compared with the new equations IPCC (2006) had smaller values for r_c (0.67), ER (0.7%), ED (95.8%), MEF (0.51) and greater values for RMSPE (43.0 g d^{-1}), ECT (3.50%) and MAE (32.9 g d^{-1}). Equation [AL-OR] developed from the complete database and tested with the HF dataset had the lowest values for r_c (0.613), MEF (0.45) and greatest values for RMSPE (45.7 g d^{-1}), ECT (9.28%), MAE (38.4 g d^{-1}) and *dr* (-0.41), indicating its lack of ability to predict CH_4 compared with the other equations and IPCC (2006).

Based on greatest r_c and smallest RMSPE, equation [HF-MC] was deemed to be the best-fit for HF diets (Table 3.4). Comparison of predicted vs. observed values for equation [HF-MC] and IPCC (2006) presented in Figure 3.1 indicates that regression slope for [HF-MC] was lower than unity (0.76; $P < 0.01$) but greater than [HF-OR] (0.53; $P < 0.01$) and the IPCC (2006) regression slope (0.49; $P < 0.01$). Regression analysis between observed and predicted values of CH_4 using equation [HF-MC] indicates better agreement ($R^2 = 0.66$; $P < 0.001$) than [HF-OR] ($R^2 = 0.64$; $P < 0.001$) and IPCC (2006) ($R^2 = 0.53$; $P < 0.001$). Plots of the regression residuals on centered predicted values of CH_4 with density shadowing at 95% for equation [HF-MC], [HF-OR] and IPCC (2006) are presented in Figure 3.2. Significant bias for slope was detected for [HF-MC] with a bias of -22.3 g d^{-1} at the maximum value predicted (316.9 g d^{-1}) and a bias of 13.3 g d^{-1} at the minimum value predicted (30.6 g d^{-1}) (Table 3.5). Significant bias for intercept and slope was detected for [HF-OR] with a bias of -22.7 g d^{-1} at the maximum value predicted (293.9 g d^{-1}) and a bias of 19.3 g d^{-1} at the minimum value predicted (88.1 g d^{-1}). For IPCC (2006) significant intercept bias was detected with 0.5 g d^{-1} at the maximum value predicted (258.2 g d^{-1}) and -14.8 g d^{-1} at the minimum value predicted (75.6 g d^{-1}). Overall, equation [HF-MC] performance was superior to IPCC (2006) because the predicted values from equation [HF-MC] were closer to real values than predicted values from IPCC (2006).

The study of Ricci et al. (2013), which had a forage proportion similar to our HF dataset (79.5 vs. 71.9%), compared predictions from their models based on GEI and DMI against predictions of IPCC (2006) and reported RMSE of 43.9, 46.2 and 56.3 (g d^{-1}), respectively. These values are greater than values reported in the present study. Moraes et al. (2014), using a specific database for heifers and steers, developed hierarchical models. For heifers, the first level model only considered GEI, the second level model considered GEI and NDF (%) and the third level model considered GEI, NDF (%) and BW. Model L1 obtained a lower RMSPE (21.7 g d^{-1}) than model L2 and L3 (22.5 and 22.1 g d^{-1}, respectively). These models also had lower RMSPE than IPCC (2006; 22.8 g d^{-1}). The L1 and L2 models for steers only considered GEI while L3 considered GEI and BW. The RMSPE values obtained for steer models were lower than values obtained for heifers (17.9; 17.9, 16.5, respectively and IPCC: 21.0 g d^{-1}). Values of RMSPE for heifers and steers presented by Moraes et al. (2014) are lower than values presented in the current study for the HF equations but greater than equations [LF-MC] and [LF-OR] for LF diets. Moraes et al. (2014) did not report dietary forage content; however, the distribution of NDF (%) and ADF (%) reported indicate that the database used represented data mainly for HF diets.

Table 3.4. Evaluation of equations to predict CH_4 production from beef cattle using the original high- and low forage datasets.

Equation ID	r_c	RMSPE	ECT%	ER%	ED%	MEF	MAE	*dr*
High-forage								
[HF-OR]	0.724	39.1	5.00	4.50	90.50	0.60	30.2	-0.32
[HF-MC]	0.813	36.4	0.20	3.80	96.00	0.60	27.4	-0.29
IPCC 2006	0.669	43.0	3.50	0.70	95.80	0.51	32.9	-0.35
[AL-OR]	0.613	45.7	9.28	2.19	88.54	0.45	38.4	-0.41
Low forage								
[LF-OR]	0.907	13.7	0.10	0.20	99.70	0.83	11.0	-0.20
[LF-MC]	0.924	12.6	0.10	0.10	99.80	0.86	10.7	-0.20
IPCC 2006	0.293	43.2	5.50	36.50	55.00	-0.65	31.2	-0.57
[AL-OR]	0.848	17.4	0.29	0.10	99.61	0.73	13.7	-0.25

Note: *dr*: index of agreement; ECT%, error due to overall bias of prediction as percentage of mean square prediction error (MSPE); ED%, random or disturbance error as percentage of MSPE; ER%, error due to deviation of the regression slope from unity as percentage of MSPE; MAE: mean absolute error (g d^{-1}); MEF: model efficiency; r_c : concordance correlation; RMSPE: root mean square prediction error (g d^{-1}).

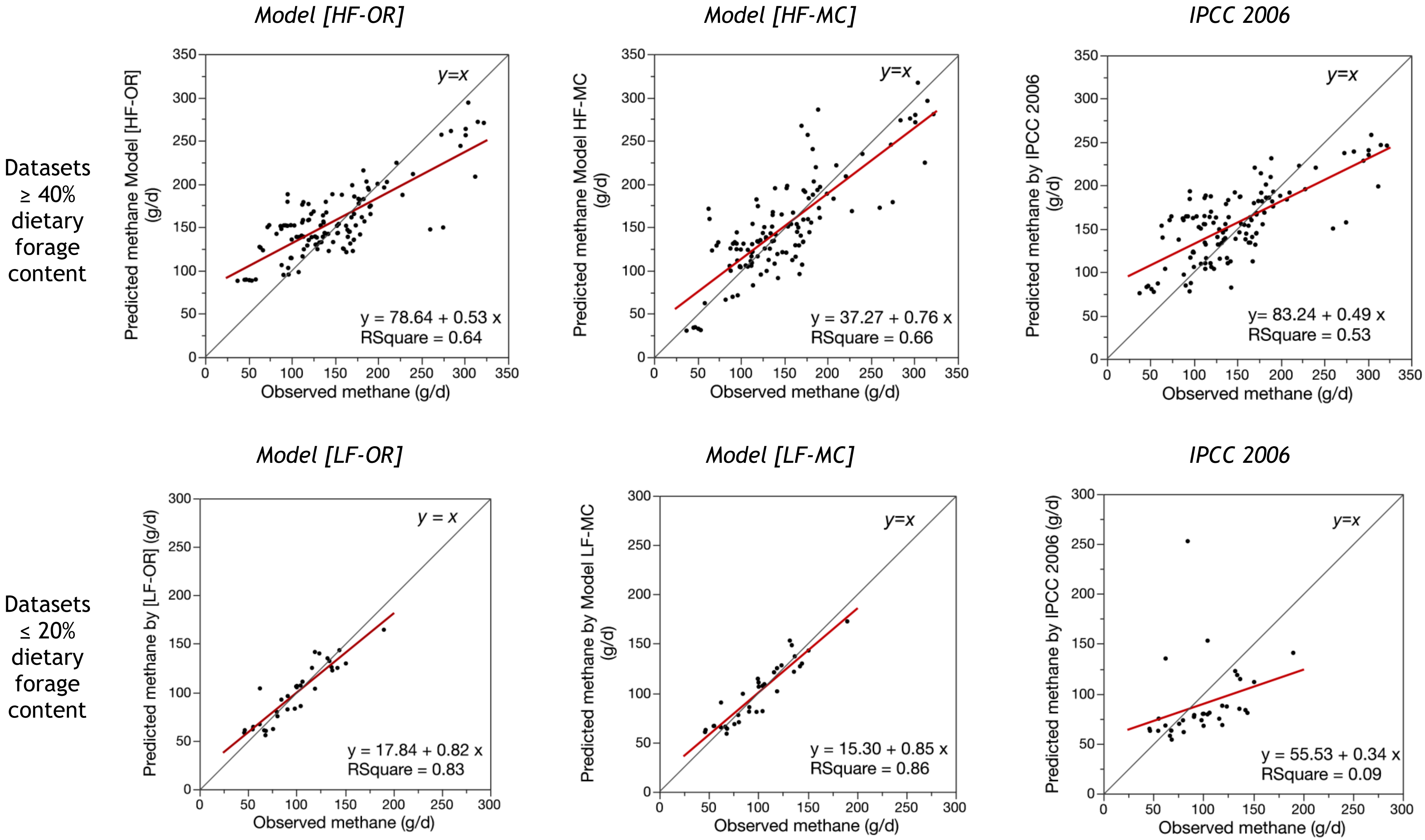

Fig. 3.1. Plots of the relationship between predicted and observed enteric methane production (g d^{-1}) for beef cattle fed high- and low forage diets using the best-fit equations from the study compared with IPCC (2006) predictions.

No other studies have developed CH_4 prediction models for feedlot cattle, thus the LF equations were only compared with IPCC (2006) predictions and equation [AL-OR] (Table 3.4). The equation [LF-MC] had greater r_c (0.924), MEF (0.86), and ED (99.80%) and smaller RMSPE (12.6 g d^{-1}), MAE (10.7 g d^{-1}) and *dr* (-0.20) than IPCC (2006) and [AL-OR]. Equations [LF-OR] and [LF-MC] had smaller ECT (0.10%) and equation [LF-MC] had lower ER (0.10%) than IPCC (2006) (36.5%) but was similar to [AL-OR] (0.10%). Performance of IPCC (2006) using the LF dataset had the lowest values of r_c (0.293), ED (55.00%), MEF (-0.65) and *dr* (-0.57) while values for RMSPE (43.2 g d^{-1}) and ER (36.50%) were greatest compared with the new equations. The analysis of r_c, RMSPE and MEF showed that equation [AL-OR] developed from the complete database had poorer performance than the LF equations; but were better than the IPCC (2006) equation.

Figure 3.1 presents regression analyses between predicted and observed values of CH_4. The regression slope for IPCC (2006) lacked agreement ($R^2 = 0.09$; $P < 0.08$), conversely equation [LF-MC] was close to unity (0.86; $P < 0.01$) and higher than [HF-OR] (0.83; $P < 0.01$). Plots of the regression residuals on centered predicted values of CH_4 for IPCC (2006), equations [LF-MC] and [LF-OR] are presented in Figure 3.2. No significant mean or linear bias (Table 3.5) was detected for equation [LF-MC] and [LF-OR] for the LF diets. In comparison, IPCC (2006) had significant mean bias and a linear bias of -108.1 g d^{-1} at the maximum predicted value (252.8 g d^{-1}) and 35.9 g d^{-1} at the minimum predicted value (53.9 g d^{-1}).

Table 3.5. Evaluation of bias for the prediction equations.

Equation ID	Average ($g\ CH_4\ d^{-1}$) [a]	Mean bias	Linear bias	*P* value mean bias	*P* value linear bias	Minimum bias ($g\ d^{-1}$)	Maximum bias ($g\ d^{-1}$)
High-forage							
[HF-OR]	156.8	-8.71	0.20	0.01	0.02	-22.7	19.3
[HF-MC]	149.6	-1.49	-0.12	0.65	0.03	13.3	-22.3
IPCC 2006	156.1	-8.06	0.08	0.04	0.37	-14.8	0.5
Low forage							
[LF-OR]	99.3	0.48	0.02	0.85	0.79	-0.5	1.9
[LF-MC]	100.1	-0.42	0.01	0.85	0.88	-0.9	0.4
IPCC 2006	89.6	10.10	-0.72	0.08	0.00	35.9	-108.1

Note: [a]CH_4, enteric methane.

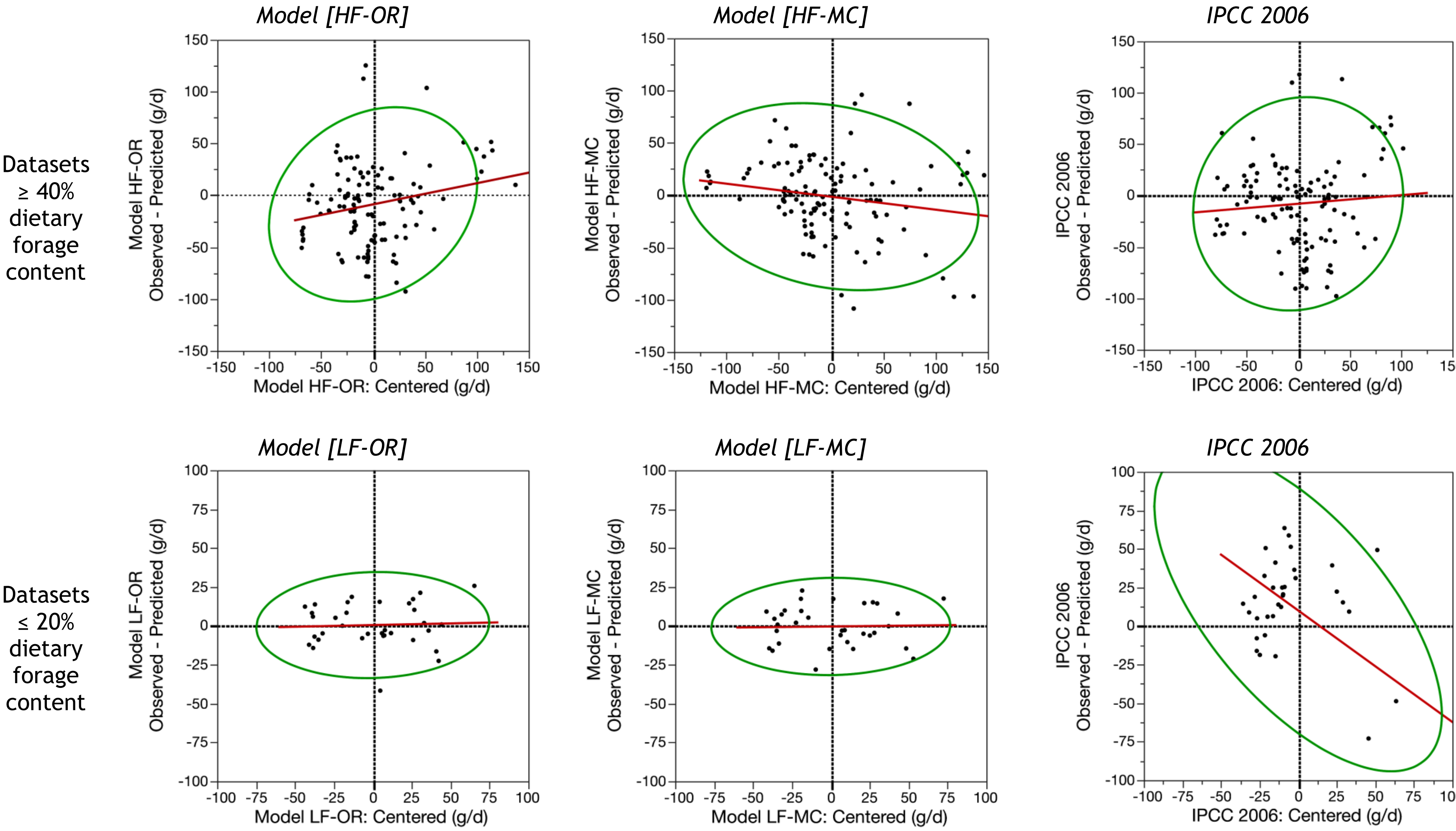

Fig. 3.2. Plots of observed minus predicted CH_4 production (g d^{-1}) vs. centered enteric methane production for equations [HF-MC], [LF-MC] and IPCC (2006) using the high-forage dataset (≥ 40% dietary DM) and low forage dataset (≤ 20% dietary DM).

3.4. Conclusion

Treatment means from a wide range of beef cattle studies conducted in numerous countries were used to build databases with two different ranges of dietary forage content representing HF diets fed to breeding stock and growing cattle and LF diets fed to feedlot cattle. Accounting for forage proportion resulted in equations with greater precision for estimating CH_4 production from beef cattle compared with IPCC (2006) Tier 2 methodology and equations developed from a combined database that was not specific to forage content.

Use of MC techniques to resample the original datasets, while maintaining the statistical characteristics of the original population, was useful for overcoming the limited data, particularly for feedlot cattle fed LF diets. Cross validation and evaluation indicated that the newly developed equations, which account for nutrient intake of cattle fed diets that differ in forage proportion, can be used to predict acceptable values of CH_4 production for beef cattle. These high- and low forage equations are simple to implement as they use variables commonly reported for beef cattle feeds by commercial laboratories and do not require inputs of dietary energy content (e.g., GE, digestibility). Accurate prediction of CH_4 emission from beef cattle is crucial for the beef industry and governments to develop appropriate strategies to minimize the contribution of cattle to climate change.

Supplementary Table 3.1. Dietary variables included in both datasets.

Variable	Unit	Abbreviation
Body weight	kg	BW
Organic matter	% DM	OM (%)
Crude protein	% DM	CP (%)
Neutral detergent fiber	% DM	NDF (%)
Acid detergent fiber	% DM	ADF (%)
Non-fiber carbohydrate [a]	% DM	NFC (%)
Hemicellulose [b]	% DM	HC (%)
Cellulose [c]	% DM	CEL (%)
Fat [d]	% DM	Fat (%)
Sugar	% DM	Sugar (%)
Starch	% DM	Starch (%)
Gross energy	MJ kg^{-1} DM	GE
Dry matter intake	kg day^{-1}	DMI
Forage daily intake	kg DM day^{-1}	-
CP daily intake	kg day^{-1}	CP
NDF daily intake	kg day^{-1}	NDF
ADF daily intake	kg day^{-1}	ADF
NFC daily intake	kg day^{-1}	NFC
HC daily intake	kg day^{-1}	HC
CEL daily intake	kg day^{-1}	CEL
Fat daily intake	kg day^{-1}	fat
Sugar daily intake	kg day^{-1}	sugar
Starch daily intake	kg day^{-1}	starch
Gross energy daily intake	MJ	GEI
CP:NDF	-	CP:NDF
NFC:NDF	-	NFC:NDF
Starch:NDF	-	starch:NDF
Daily production of methane	g day^{-1}	CH_4

Note: [a]NFC = 100 - (NDF + CP + fat + ash).
[b]HC = (NDF-ADF).
[c]CEL = ADF-ADL).
[d]Measured as ether extract.

Supplementary Table 3.2. Summary of studies included in database.

Author(s)	Animal category	Breed	CH_4 measurement method	CH_4 (g d^{-1})	Country
Beauchemin and McGinn (2005)	Steers	Angus	Chambers	62.1	Canada
Beauchemin and McGinn (2006a)	Heifers	Angus	Chambers	141.5	Canada
Beauchemin and McGinn (2006b)	Steers	Angus	Chambers	108.0	Canada
Beauchemin et al. (2007a)	Steers	Angus	Chambers	119.6	Canada
Beauchemin et al. (2007b)	Steers / heifers	Angus	Chambers	98.7	Canada
Boadi and Wittenberg (2002)	Heifers	Holstein and Charolais × Simmental	SF_6[a]	127.6	Canada
Boadi et al. (2001)	Steers	Red Angus	SF_6	169.1	Canada
Boadi et al. (2004)	Steers	Continental × British crossbred	SF_6	59.4	Canada
Boland et al. (2013)	Heifers	Limousin	SF_6	127.0	Ireland
Chaves et al. (2006)	Heifers	Angus	SF_6	150.9	Canada
Chung et al. (2013)	Heifers	Crossbred	Chambers	90.0	Canada
Chung et al. (2011)	Steers	Holstein	SF_6	261.0	Canada
Cooprider et al. (2011)	Steers	Angus cross steers	Chambers	281.8	USA
Doreau et al. (2011)	Bulls	Blond d'Aquitaine	SF_6	62.3	France
Fiorentini et al. (2014)	Steers	Nellore	SF_6	91.7	Brazil
Fitzsimons et al. (2013)	Heifers	Simmental	SF_6	260.0	Ireland
Grainger et al. (2008)	Steers	Holstein	SF_6	399.0	Australia
Gutierrez et al. (2007)	Steers	Holstein	SF_6	113.8	USA
Hales et al. (2012)	Steers	Jersey	Chambers	38.8	USA
Hales et al. (2013)	Steers	Jersey	Chambers	46.1	USA
Hales et al. (2014a)	Steers	Cross	Portable head boxes	93.3	USA
Hales et al. (2014b)	Steers	Cross	Portable head boxes	107.5	USA
Hart et al. (2009)	Heifers	Charolais cross	SF_6	138.0	Ireland
Hegarty et al. (2007)	Steers	Angus	SF_6	142.3	Australia
Henry et al. (2015)	Heifers	Crossbreed	SF_6	87.5	USA
Hosoda et al. (2012)	Steers	Holstein	Chambers	99.9	Japan
Hulshof et al. (2012)	Steers	Nellore × Guzera	SF_6	85.0	Netherlands

Hunerberg et al. (2013a,b)	Heifers	Crossbred	Chambers	119.0	Canada
Jiao et al. (2013)	Heifers	Holstein	Chambers	96.4	UK
Jones et al. (2011)	Steers	Angus	FTIR[b]	125.1	Australia
Jordan et al. (2006a)	Steers	Charolais - Limousin cross	SF_6	55.4	Ireland
Jordan et al. (2006b)	Heifers	Charolais - Limousin cross	SF_6	55.4	Ireland
Lee et al. (2015)	Heifers	Crossbred	Chambers	183.0	Canada
Li et al. (2012)	Steers	Holstein	Chambers	82.4	USA
Lila et al. (2005)	Steers	Holstein	Chambers	77.0	Japan
Lovett et al. (2003)	Heifers	Charolais cross	SF_6	112.2	Ireland
Mc Geough et al. (2010a)	Steers	Continental crossbred	SF_6	180.0	Ireland
Mc Geough et al. (2010 b)	Steers	Crossbred	SF_6	228.0	Ireland
McGinn et al. (2004)	Steers	Holstein	Chambers	129.0	Canada
McGinn et al. (2009)	Steers	Hereford	SF_6	177.0	Canada
Molano et al. (2006)	Steers	Hereford × Friesian	SF_6	89.1	New Zealand
Newbold et al. (2014)	Steers	Holstein	Chambers	86.8	Netherlands
Pinares-Patiño et al. (2003)	Steers	Charolais	SF_6	204.4	France
Romero-Pérez et al. (2014)	Heifers	Angus	Chambers	203.0	Canada
Romero-Pérez et al. (2015)	Heifers	Angus	Chambers	157.9	Canada
Stackhouse et al. (2011)	Steers	Angus	Chambers	68.4	USA
Stackhouse et al. (2013)	Steers	Angus	Chambers	239.0	USA
Staerfl et al. (2012)	Steers	Brown Swiss × Limousin	Chambers	37.4	Switzerland
Troy et al. (2015)	Steers	Charolais and Luing	Chambers	194.3	UK
Vyas et al. (2014a)	Heifers	Crossbred	Chambers	177.5	Canada
Vyas et al. (2014b)	Heifers	Crossbred	Chambers	138.5	Canada
Vyas et al. (2015)	Heifers	Crossbred	Chambers	187.8	Canada
Vyas et al. (unpublished)	Steers	Crossbred	Chambers	125.9	Canada

Note: [a]SF_6 : Sulfur hexafluoride.
[b]FTIR: Fourier transform infrared spectroscopy.

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CHAPTER 4. Estimating enteric methane production for beef cattle using empirical prediction models compared with IPCC Tier 2 methodology[3]

4.1. Introduction

The agricultural sector contributes 8% (59 Mt CO_2 equivalent in 2014) of greenhouse gas emissions in Canada, of which 42% (25 Mt CO_2 equivalent in 2014) is mainly from CH_4 produced from enteric fermentation (Environment and Climate Change Canada 2016). Within the livestock sector, beef cattle are the largest source of emissions both in Canada and globally. Beef production contributes 41% of global livestock emissions (Gerber et al. 2013), while beef accounts only for about 25% of total agricultural emissions in Canada (Environment and Climate Change Canada 2016).

The Canadian beef industry is complex and diverse in size and scale (Sheppard et al. 2015, Alemu et al. 2016, Legesse et al. 2016). In simple terms, the system starts with breeding herds (cow–calf sector) that produce calves for subsequent backgrounding and finishing. The cows and their suckling calves are generally maintained on pasture during the summer grazing period, calves are weaned in the fall, and pregnant cows are over-wintered using supplemental feed. Weaned calves are mainly backgrounded on forage-based diets in feedlots or as stocker cattle on pasture for varying lengths of time before they are finished in feedlots using grain-based diets (Beauchemin et al. 2010, Alemu et al. 2016).

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Over the lifespan of a beef animal, there are continuous changes in diet composition, which are driven by the availability and price of feed and the need to balance diets to meet requirements based on the animal age, physiological stage of maturity and environmental conditions. Diet composition affects DMI and the ruminal microbial population, and hence ruminal fermentation end products, including CH_4. Forage diets promote acetate production in the rumen, which results in more hydrogen being available as a precursor for methanogenesis (Janssen 2010). In contrast, high-grain diets promote propionate production, which uses hydrogen and produces less CH_4. In beef cattle, CH_4 production represents 2 to 12% of gross energy consumed depending upon level of intake and composition of the diet (Johnson and Johnson 1995).

The United Nations Framework Convention on Climate Change requires countries to provide estimates of all GHG emissions and their uncertainties using Intergovernmental Panel on Climate Change (IPCC, 2006) methodology. Accuracy of the IPCC Tier 2 methodology is applicable for high-forage diets but inaccurate for diets with high proportion of concentrates and estimation of enteric CH_4 production for beef cattle is consequently associated with large uncertainty (15 to 33%; Karimi-Zindashty et al. 2016). Nevertheless, Environment Canada uses the IPCC (2006) Tier 2 methodology to produce its national annual inventory report (Environment Canada 2014). Specifically, GEI of a representative animal for each class of beef cattle is estimated, and then multiplied by a CH_4 emission factor (Ym, % of GEI on an energy basis). The emission for each class of animal is then multiplied by the population of animals within each class and summed to estimate the total CH_4 emission for the beef sector. The IPCC provides a default Ym value of 6.5 ± 1% for beef cattle consuming diets with less than 900 g concentrate kg^{-1}, and Ym of 3 ± 1% for finishing cattle consuming more than 900 g of concentrate per kg DM^{-1}. Country-specific Ym values can be used to make inventories when supporting justification is available. The Ym value used is critical because it has a direct effect on estimated CH_4 production and is the main source of uncertainty in estimating cattle emissions in greenhouse gases inventories (Karimi-Zindashty et al. 2011).

Various empirical models for predicting CH_4 production from beef cattle have been published (Ellis et al. 2007, 2009; Yan et al. 2009; Ricci et al. 2013; Moraes et al. 2014; Escobar-Bahamondes et al. 2016b). Using a database for beef cattle, Escobar-Bahamondes et al. (2016a) showed that many equations lacked accuracy, as they were not specific for high-forage or high-grain diets. Equations were identified that predicted CH_4 production as well as or better than the IPCC Tier 2 methodology. The difference between using models that account for changes in diet composition compared with IPCC (2006) methodology for estimating CH_4 production and Ym from beef cattle in Canada is unknown. The first objective of this study was to estimate CH_4 emissions (g d^{-1} and Ym) for beef cattle in Eastern compared to Western Canada using empirical models in contrast to the IPCC (2006) Tier 2 methodology. The second objective was to estimate variability and uncertainties based in conversion of values of model predictions of CH_4 to Ym due to changes in BW of animals, feed intake and diet composition over the production cycle of cattle.

4.2. Methods

4.2.1. General overview

Most CH_4 prediction models require knowledge of animal class, BW, feed intake and diet composition. Thus, it is necessary to develop scenarios to represent beef cows and growing cattle and their respective diets during their productive lifespan. Typical scenarios were developed monthly for mature beef cows and growing steers in Eastern and Western regions of Canada to reflect differences in diet composition, BW change, and management. Due to their lower population size, bulls were not considered, while it was assumed that model comparisons for growing-finishing heifers would be similar to those for steers. Calves were not considered because they produce little CH_4. Empirical models that consider diet composition were used to predict daily CH_4 production (g d^{-1} and Ym) of individual animals by month.

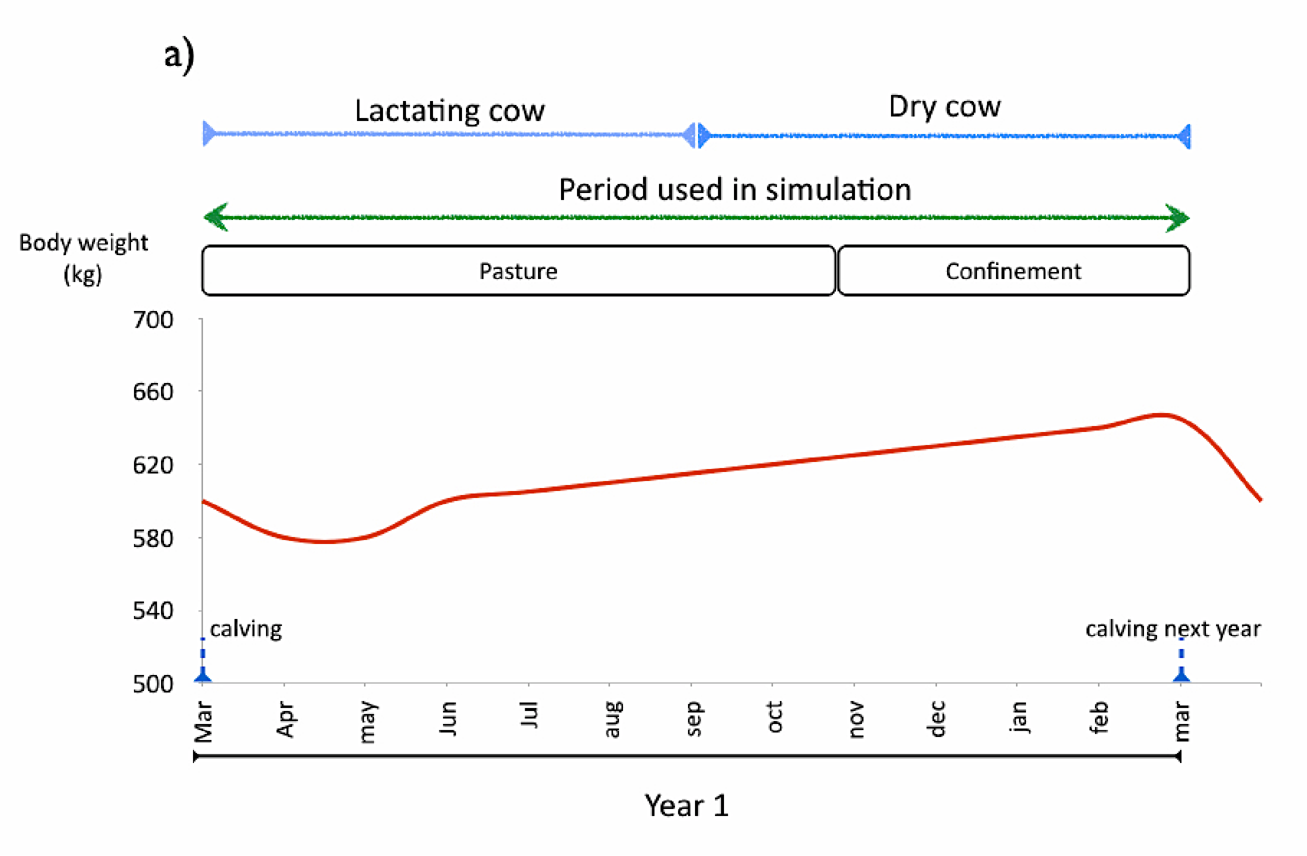
4.2.2. The beef production system and diets

The Canadian beef production system is based entirely on Bos taurus breeds and is comprised of three distinct components: cow–calf herds that produce calves, calf growing operations (stocker calves and yearlings on pasture, backgrounding in confinement), and finishing feedlots. Cow-calf and calf growing operations utilize high fibre diets including grazed pastures, harvested forages and by-product feeds. The finishing phase is largely conducted in feedlots using high grain diets. Many different management practices and diets for growing and finishing cattle are used in Canada (Sheppard et al. 2015; Legesse et al. 2016). As the focus of the current study was to explore variability and uncertainties in CH_4 prediction due to the differing calculation approaches, it was necessary to develop typical production schemes to represent mature cows and growing cattle (steers) and their respective diets throughout the production cycle.

The production schemes used for beef cows and steers are based on Legesse et al. (2016) and presented in Fig. 4.1a. Each scheme was comprised of individual stages to account for changes in BW, diet composition and management (grazing, confinement). Schemes for Eastern and Western Canada differed slightly to reflect regional differences in management and diets (Sheppard et al. 2015). Although both native and tame pastures are grazed by beef cattle in Western Canada, only tame pasture was considered because of the lack of detailed nutritional information for native pasture.

The beef cow simulation was conducted over a 12-month season (parturition in March) with two 6-month stages (lactating, non-lactating) to reflect changes in DMI (due to additional nutrient requirements for lactation), BW and diet composition (Figure 1a). The initial and final BW of cows were obtained from Sheppard et al. (2015). A milk yield during the lactation phase of 1,600 L, was assumed, equivalent to 8 kg d^{-1} at peak lactation (Mathison 1993).

For growing-finishing beef cattle, the simulation started with weaned calves (November, 8 mo of age). A yearling steer scenario was selected to allow for exploration of various types of diets (high-forage, pasture, and high-concentrate). According to Legesse et al. (2016), this scenario represents about one-third of calf production in Canada. Simulations were conducted in Eastern and Western regions to reflect differences in diet ingredients and age at slaughter. Steers were assumed to be fed a high-forage diet under confinement (backgrounder) from November to March when mean ambient temperature was below 0 °C. From April to October, the steers had access to tame pasture, and from November until the end of their productive life, the steers were fed a high-concentrate diet in a feedlot (Figure 4.1b). The BW and average daily gain of growing animals during the various phases were from Sheppard et al. (2015) and Legesse et al. (2016).



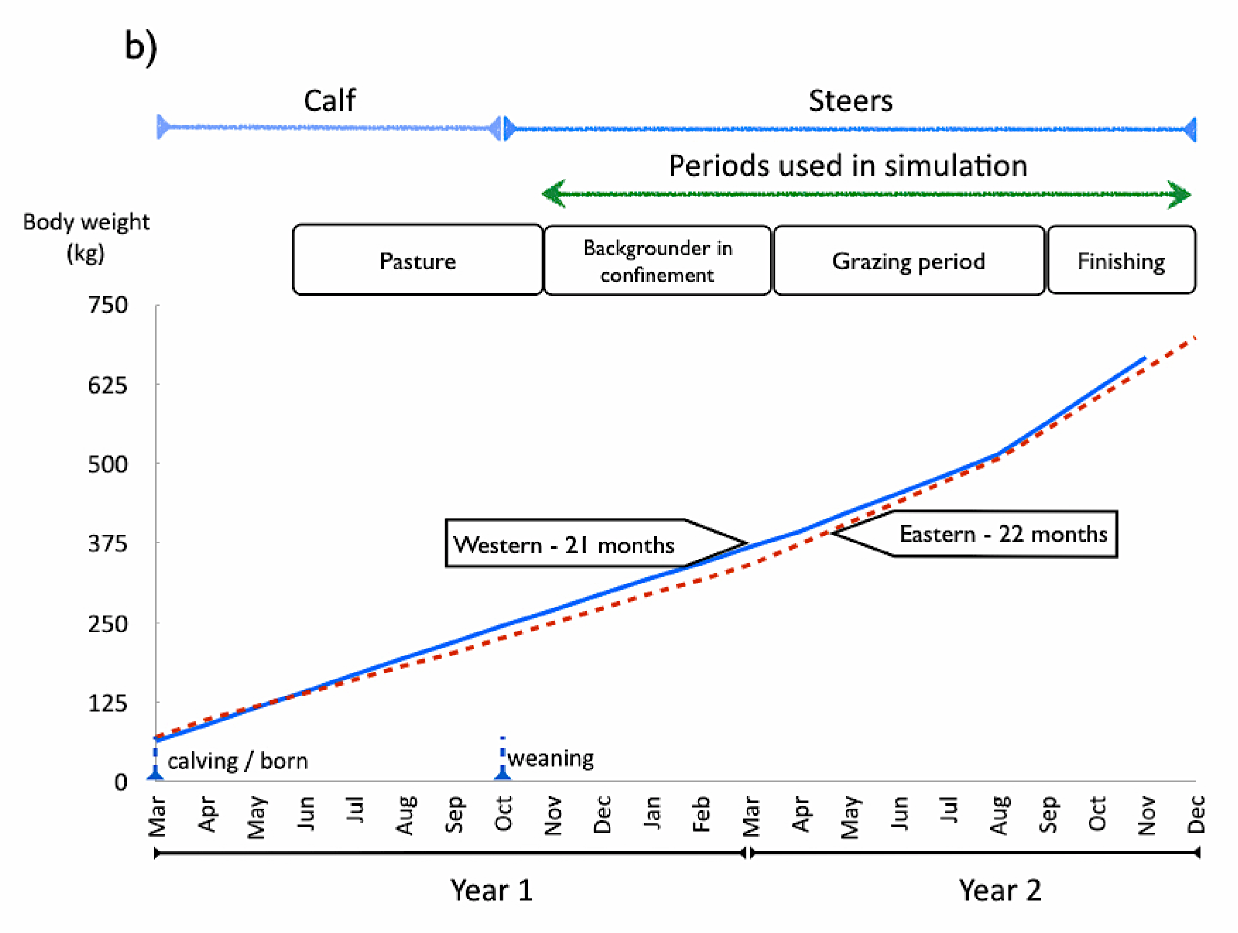


Figure 4.1. Production schemes used in the simulations for a) beef cows and b) growing-finishing steers.

4.2.3. Diet composition

Representative diets were selected for each phase of each production scheme. These diets accounted for differences in feed sources used in Western and Eastern regions of Canada. In the West, barley grain, barley silage and grass-legume hay were the main feeds, whereas in the East, diets included corn grain, corn silage, alfalfa hay and soybean meal (Mathison 1993, Beauchemin and McGinn 2005, Shepard et al. 2015, Legesse et al. 2016). The forage:concentrate ratio of the diets for the various classes of cattle varied throughout the production cycle as outlined by Legesse et al. (2016).

The nutritional composition of dietary ingredients was estimated from Abouguendia (1990), the Beef Cattle Nutrient Requirement Model (National Academies of Sciences, Engineering, and Medicine [NASEM] 2016), Cowbytes 5.0(c) and the National Animal Nutrition Program for America and Canada ([Online] Available: http://nanp-nrsp-9.org [2016 Feb. 01]). A summary of the feed composition data and diets used in the simulations is presented in supplementary Tables 1 and 2.

Most enteric CH_4 prediction equations require an estimate of DMI, which was estimated monthly for each class of cattle using the Beef Cattle Nutrient Requirement Model (NASEM 2016). Representative diets were created using peer-reviewed papers that reported detailed information about beef production in Canada (Beauchemin and McGinn 2005; Beauchemin et al. 2010; Alemu et al. 2011; Legesse et al. 2011; Sheppard et al. 2015; Legesse et al. 2016). The variables estimated were: BW (kg), forage intake (% DM), organic matter (% DM), crude protein (CP, % DM), neutral detergent fiber (NDF, % DM), acid detergent fiber (ADF, % DM), non-fiber carbohydrate (NFC, % DM; NFC = 100 - (NDF + CP + fat + ash)), hemicellulose (HC, % DM; HC = NDF-ADF), cellulose (CEL, % DM; CEL = ADF-ADL), fat (% DM), sugar (% DM), starch (% DM), gross energy (GE, MJ kg^{-1} DM), digestible energy (DE, MJ kg^{-1} DM), metabolizable energy (ME, MJ kg^{-1} DM), and daily intakes of each of the dietary constituents including: DMI (kg d^{-1}), forage (kg DM d^{-1}), CP (kg DM d^{-1}), NDF (kg DM d^{-1}), ADF (kg DM d^{-1}), NFC (kg DM d^{-1}), HC (kg DM d^{-1}), CEL (kg DM d^{-1}), fat (kg DM d^{-1}), sugar (kg DM d^{-1}), starch (kg DM d^{-1}), GEI (MJ d^{-1}), MEI (MJ d^{-1}). The GE content was calculated according to NASEM (2016).

4.2.4. Estimation of methane production.

IPCC (2006) Tier 2 methodology and 16 models that consider dietary nutrient composition, daily intakes and BW were used to predict enteric CH_4 for cows and steers using the compiled information for diets and intake. The equations used were those identified by Escobar-Bahamondes et al. (2016a,b) as being most accurate (best-fit) for high-forage (≥ 40% DM; HF) or low-forage (≤ 20% DM; LF) diets. Detailed descriptions of equations used in this study are presented in Table 1. Not all models were appropriate for beef cows or all phases of steer growth, thus only relevant models were used for each class and phase of cattle production. Specifically, few models have been developed for mature beef cows, and some equations are only accurate for heifers, or for growing cattle fed high- or low-forage diets. Daily CH_4 emissions (g d^{-1}) were calculated monthly using all relevant models for each category of beef cattle. Values of CH_4 were transformed to energy assuming 55.6 MJ kg^{-1} CH_4 and expressed as Ym (% GEI).

Table 4.1. Equations used to predict enteric CH_4 production.

Id and Source		Model	Type of model	Use in this study
High-forage contents diets				
IPCC (2006) - Tier 2	CH_4 =	(DMI × 18.5 (MJ kg^{-1} DM) × Y_m) /55.65 (MJ kg^{-1} CH_4)	I	Cow and steers
SAL - Moraes et al. (2014)	CH_4 =	-0.221 + 0.048 × GEI + 0.005 × BW	I	Steers
N - Ellis et al. (2009)	CH_4 =	2.68 - 1.14 × (starch:NDF) + 0.786 × DMI	II	Cows or steers
HAL - Moraes et al. (2014),	CH_4 =	-1.487 + 0.046 × GEI + 0.032 × NDF (%) + 0.006 × BW	II	Cows
14b - Ellis et al. (2007)	CH_4 =	2.94 + 0.0585 × MEI + 1.44 × ADF - 4.16 × lignin	II	Cow and steers
iiib - Yan et al. (2009)	CH_4 =	[[1.749 – 12.18 ME/GE + 10.74 DE/GE] GEI – 14.0] × 0.66] × 0.0556	II	Cow and steers
HFOR - Escobar-Bahamondes et al. (2016b)	CH_4 =	71.5(± 11.45) + 0.12(± 0.03) × BW + 0.10(± 0.01) × DMI^3 - 244.8(± 56.44) × fat^3	III	Cow and steers
HFMC - Escobar-Bahamondes et al. (2016b)	CH_4 =	25.9(± 0.54) + [0.13(±0.001) × BW] + [145.4 (±1.31) × fat] + [10.3(±0.16) × $(NDF\text{-}ADF)^2$]+ [0.1(±0.00) × DMI^3] – [27.4 (±0.20) × (starch:NDF)]	III	Cow and steers
Finishing diets				
IPCC (2006) - Tier 2	CH_4 =	(DMI × 18.5 (MJ kg^{-1} DM) × Y_m) /55.65 (MJ kg^{-1} CH_4)	I	Steers
A - Ellis et al. (2009)	CH_4 =	2.29 + 0.670 × DMI	I	Steers
SGEL - Moraes et al. (2014)	CH_4 =	0.743 + 0.054 × GEI	I	Steers
SDL - Moraes et al. (2014)	CH_4 =	0.743 + 0.054 × GEI	I	Steers
9b - Ellis et al. (2007)	CH_4 =	0.357 + 0.0591 × MEI + 0.0500 × forage (%)	I	Steers
I - Ellis et al. (2009)	CH_4 =	2.72 + 0.0937 × MEI + 4.31 × CEL - 6.49 × HC - 7.44 × fat	II	Steers
GEI - Ricci et al. (2013)	CH_4 =	74.34 + 0.57 × GEI - 10.61 × feed - 69.67 × stage - 0.22 × GEI × feed + 0.57 × GEI × stage	II	Steers
LFOR - Escobar-Bahamondes et al. (2016b)	CH_4 =	-26.4(±20.17) + 0.21(±0.04) × BW + 30.1(±11.83) × CP - 70.5(±25.48) × fat^2 + 10.1(±5.12) × $(NDF\text{-}ADF)^3$	III	Steers
LFMC - Escobar-Bahamondes et al. (2016b)	CH_4 =	-10.1(±0.62) + 0.21(± 0.001)×BW + 0.36(±0.003)×DMI^2 - 69.2(±1.65)×fat^3 + 13.0(±0.45)×(CP:NDF) - 4.9(±0.07) × (starch:NDF)	III	Steers

Note: ADF, acid detergent fiber (kg d^{-1}); AL, animal level; BW, body weight (kg); CEL, cellulose (kg d^{-1}); DE, digestible energy (MJ kg^{-1} DM); DL, dietary level; DMI, dry matter intake (kg d^{-1}); GE, gross energy (MJ kg^{-1} DM); GEI, gross energy intake (MJ d^{-1}); GEL, gross energy level; H, heifers; ME, metabolizable energy (MJ kg^{-1} DM); MEI, metabolizable energy intake (MJ d^{-1}); NDF, neutral detergent fiber (kg d^{-1}); S, steers; stage, physiological stage (nonlactating or lactating);Y_m, Methane conversion factor (6.5% for diets >90 g forage kg^{-1} DM, 3.0% for diets ≤90 g forage kg^{-1} DM).

4.2.5. Datasets and analysis.

Datasets were generated for each animal category (cows, steers). Each record (row) within the dataset represented the animal within a region (East, West) on a monthly basis. The variables (columns) provided information on general management, BW, type of diet, dietary forage content (% DM), chemical composition of the diet and nutrient intakes. The dataset for beef cows contained 24 records (12 mo × 2 regions) and 40 variables whereas the dataset for steers contained 27 records (8 to 22 mo for East and 8 to 21 mo for West). The information for each record was then used with the appropriate algorithm to predict CH_4 (g d^{-1} and Ym).

Mean daily CH4 emissions (g d^{-1}) and Ym values, both estimated monthly, were compared within each phase of production for Eastern vs. Western Canada by averaging over all models. Estimates were compared against the IPCC prediction and among models within each production phase. The variability of Ym between models was determined using coefficient of variation (CV) and uncertainty (%). The CV and uncertainty were calculated for each model by production stage for mature cows and growing cattle. The uncertainty was calculated according to Karimi-Zindashty et al. (2012) as the 95% confidence interval/mean × 100%.

All comparisons were conducted using a Kruskal-Wallis test and nonparametric multiple comparisons between means were made by the Steel-Dwass all pairs test or Wilcoxon each pair test (Zar 2010; SAS 2015). Significance was declared at $P \leq 0.05$. Statistical software used was JMP© 12, SAS Institute, Cary, NC (SAS 2015).

4.3. Results and discussion

4.3.1. The models

The models used were organized from lower to higher degree of complexity with indication of the appropriate use for high and low forage diets (Table 1). The models could be categorized into 3 groups: 1) linear models that use one or two variables, especially GEI, DMI and BW (e.g., IPCC, SAL, A, SGEL and SDL), 2) linear models that consider a number of dietary variables (e.g., HAL, 14b, iiib, 9b, I and GEI), and 3) polynomial models that generate a more complex expression of dietary and animal variables (e.g., HFOR, HFMC, LFOR and LFMC).

Predictions from the IPCC model are based on GEI; however GEI values are often not reported in feed analysis. The IPCC (2006) suggests using a default value of 18.45 MJ kg^{-1} of DM when GE content of feeds is not available. Using a constant GE value results in the equation being only sensitive to changes in DMI and not to changes in composition of diets. Thus, using the IPCC model, Ym is constant and changes in CH_4 are strictly due to changes in DMI. The other models were developed using mixed datasets for dairy and beef cows (Ricci et al. 2013), heifers and steers (Ellis et al. 2009, Moraes et al. 2014, Escobar-Bahamondes et al. 2016b) or models that did not clearly specify the origin of dataset (Ellis et al. 2007). These models were selected for use in the present study based on their superior accuracy and precision for beef cattle fed high-forage or high- grain diets (Escobar-Bahamondes et al. 2016a; Table 4.1). However, the database used by Escobar-Bahamondes et al. (2016a) to evaluate the equations included very few studies using mature cows or grazing cattle. Most studies were conducted with steers or heifers in metabolism studies where growth of cattle was low or not reported. In addition a small number of studies were conducted with growing cattle in confinement fed backgrounding and finishing diets.

4.3.2. Comparison of models for beef cows

Overall predicted Ym values averaged across models for lactating (mean, 7.0%) and dry (mean, 7.3%) beef cows were similar ($P > 0.05$) for Eastern and Western regions (Table 4.2). Likewise, for lactating cows the average predicted CH_4 emissions across all models were similar (mean, 265 g d^{-1}; $P > 0.05$) for Eastern and Western regions, but emissions for dry cows were 14% greater (263 vs. 231 g d^{-1}; $P \leq 0.05$) in Western than Eastern Canada. This difference between regions for CH_4 production of dry cows when expressed as g d^{-1} but not when expressed as Ym indicates differences in DMI attributed to different BW rather than differences in the nutrient composition of diets even though dry cows in the West consumed barley-based diets compared with corn-based diets in the East (Supplementary Table 4.1).

Only a few studies have measured CH_4 production from mature cows under production conditions. Pinares-Patiño et al. (2003) used Charolais dry cows (BW, 712 kg) grazing pastures of timothy at four stages of maturity (early vegetative, heading, flowering, and senescence) and reported a range of 204 - 273 g d^{-1} of CH_4 with Ym ranging from 5.9 - 6.7%. These values are within the range reported in the present study.

The overall CV resulting from the range in model estimates of Ym for lactating cows due to monthly changes in DMI and diet composition was 24% in the East and 29% in the West (Table 4.2). The slightly lower variability for dry cows (CV = 16 to 20%)

was attributed to smaller changes in DMI and diet composition over the 6-month period compared with diets consumed during lactation.

Table 4.2. Period, BW and CH_4 production averaged across all models by region and stage production for beef cows and growing steers.

	Eastern region	Western region
Beef cows		
Lactating stage		
Period (months)	6	6
BW, kg (min - max)	600 - 617	578 - 602
Overall[a] Ym (%; mean ± SD, CV)	[b]7.0*a* ± [c]1.69, [d]24.0	[b]7.1*a* ± [c]2.09, [d]29.4
Overall CH_4 (g d^{-1}; mean ± SD, CV)	258*a* ± 66.4, 25.7	271*a* ± 79.6, 29.4
Dry stage		
Period (months)	6	6
BW, kg (min - max)	617 - 663	602 – 654
Overall Ym (%)	7.2*a* ± 1.18, 16.4	7.3*a* ± 1.48, 20.3
Overall CH_4 (g d^{-1})	231*a* ± 40.3, 17.5	263*b* ± 53.5, 20.3
Growing steers		
Backgrounder phase		
Period (months)	6	6
BW, kg (min - max)	226 - 341	245 - 393
Overall Ym (%)	6.5*a* ± 1.08, 16.6	6.4*a* ± 0.89, 13.9
Overall CH_4 (g d^{-1})	116*a* ± 20.9, 18.0	148*b* ± 21.2, 14.3
Grazing phase		
Period (months)	5	4
BW, kg (min - max)	384 - 518	424 - 514
Overall Ym (%)	6.6*a* ± 1.25, 18.9	6.5*a* ± 1.43, 22.0
Overall CH_4 (g d^{-1})	209*a* ± 46.2, 22.1	232*b* ± 52.6, 22.7
Finishing phase		
Period (months)	4	3
BW, kg (min - max)	564 - 708	564 - 667
Overall Ym (%)	4.8*a* ± 0.87, 18.1	4.8*a* ± 0.84, 17.5
Overall CH_4 (g d^{-1})	152*a* ± 29.1, 19.1	158*a* ± 27.8, 17.6

Note: [a] Means within a row without the same letter are different ($P \leq 0.05$).
[b] Mean.
[c] Standard deviation.
[d] Coefficient of variation (%).

There were important differences among models for predicting Ym values (Table 4.3) and daily CH_4 production (Table 4.4) for lactating and dry beef cows in both Eastern and Western Canada. For lactating cows in both regions, equations HAL and iiib predicted Ym values that were similar ($P > 0.05$) to those generated using IPCC methodology (Table 4.3). In contrast, in both regions HFMC predicted considerably greater ($P \leq 0.05$) Ym values compared with all other models: whereas HFOR predicted greater ($P \leq 0.05$) Ym values compared to IPCC. Equations 14b and N estimated lower Ym values than IPCC. For lactating beef cows, IPCC (2006) estimated a daily emission in the East of 248 g d^{-1}, which was similar to the range of estimates (208 to 237 g d^{-1}; $P > 0.05$) for all models except HFOR (287 g d^{-1}) and HFMC (376 g d^{-1}), which were considerably greater ($P \leq 0.05$; Table 4.4). For lactating cows in the West, IPCC estimated an emission of 257 g d^{-1}, which was similar to iiib, but greater ($P \leq 0.05$) than estimates generated by models 14b, N, and HAL and lower ($P > 0.05$) than estimates generated by HFMC and HFOR.

Regardless of region, no model predicted a Ym value similar to that of IPCC ($P \leq 0.05$; Table 4.3) for dry cows. In the East, models HFMC, HFOR, iiib and HAL predicted values greater than IPCC (9.5, 8.0, 7.6 and 7.0 vs. 6.5%, respectively). Predictions of models 14b and N were lower ($P \leq 0.05$) than IPCC. In the West, model performance for Ym was similar to that in the East. The IPCC model estimated 220 g d^{-1} of CH_4 for dry cows in the East, similar to estimates generated by HFOR, iiib and HAL (252, 241, 220 g d^{-1}, respectively; $P > 0.05$; Table 4.4) but greater than those generated by 14b and N (195 and 190 g d^{-1}; $P \leq 0.05$) and less than HFMC (299 g d^{-1}; $P \leq 0.05$). For dry cows in the West, IPCC predicted 250 g d^{-1}, which was only similar to iiib (273 g d^{-1}; $P \leq 0.05$). Other models predicted greater (HFMC, HFOR; $P \leq 0.05$) or lower estimates (HAL, 14b, N; $P \leq 0.05$).

When used for mature beef cows, the models differed in their sensitivity to changes in dietary components, as evidenced by the CV reported in Table 4.3 (Ym) and Table 4.4 (g d^{-1}) and the range in Ym presented in Figure 4.2. Equations HAL and N had the greatest stability in their responses within phase (CV < 2.5%) and across locations with HAL being closest to IPCC estimates. Although they considered variables such as NDF content, GEI (HAL only) and BW (HAL only), those equations were not very sensitive to changes in inputs and estimates of Ym were relatively constant within each of these models. Equation 14b uses MEI, ADF content, and lignin content as inputs, and despite changes in these inputs across the production phases, the predictions were relatively constant, except for Western lactating cows because dietary ADF content had greater variability (Supplementary Table 4.1). This likely is a reflection of changes in pasture maturity during the grazing season. Models HFMC and HFOR consistently predicted greater Ym and CH_4 than IPCC, and estimates from these models were also more variable within production phase. Both these models incorporate DMI and HC (NDF-ADF) as inputs expressed as polynomial variables, and BW, which varied across the year. Model iiib uses ratios between different types of energy, thus variation in DE and ME content of diets across the season caused this model to have greater variation in Ym values.

Table 4.3. Ym (% GEI) predicted from different models for mature beef cows by region and stage of production.

Models[a]	Eastern region			Western region		
	Average	SD[b]	CV[c]	Average	SD	CV
Lactating stage						
IPCC (2006) -Tier 2	6.5*c*	0.00	0.00	6.5*c*	0.00	0.00
14b - Ellis et al. (2007)	6.0*d*	0.27	4.50	5.5*d*	0.94	17.09
N - Ellis et al. (2009)	5.7*e*	0.11	1.93	5.7*d*	0.09	1.58
HFMC - Escobar-Bahamondes et al. (2016b)	10.2*a*	1.46	14.31	11.4*a*	0.98	8.60
HFOR - Escobar-Bahamondes et al. (2016b)	7.8*b*	0.52	6.67	7.9*b*	0.51	6.46
HAL - Moraes et al. (2014)	6.5*c*	0.16	2.46	6.4*c*	0.11	1.72
iiib - Yan et al. (2009)	6.5*bcde*	1.92	29.54	6.5b*cd*	1.93	29.69
Dry stage						
IPCC (2006) -Tier 2	6.5*d*	0.00	0.00	6.5*d*	0.00	0.00
14b - Ellis et al. (2007)	6.2*e*	0.05	0.81	6.0*e*	0.09	1.50
N - Ellis et al. (2009)	6.0*f*	0.06	1.00	5.9*f*	0.06	1.02
HFMC - Escobar-Bahamondes et al. (2016b)	9.5*a*	0.19	2.00	10.2*a*	0.34	3.33
HFOR - Escobar-Bahamondes et al. (2016b)	8.0*b*	0.34	4.25	8.3*b*	0.39	4.70
HAL - Moraes et al. (2014)	7.0*c*	0.14	2.00	6.7*c*	0.05	0.75
iiib - Yan et al. (2009)	7.6*bc*	0.85	11.18	7.7*bc*	0.83	10.78

Note: [a] Within a column, models with different letters differ ($P \leq 0.05$).

[b] Standard deviation.

[c] Coefficient of variation (%).

Table 4.4. Methane (g d^{-1}) predicted from different models for mature beef cows by region and stage of production.

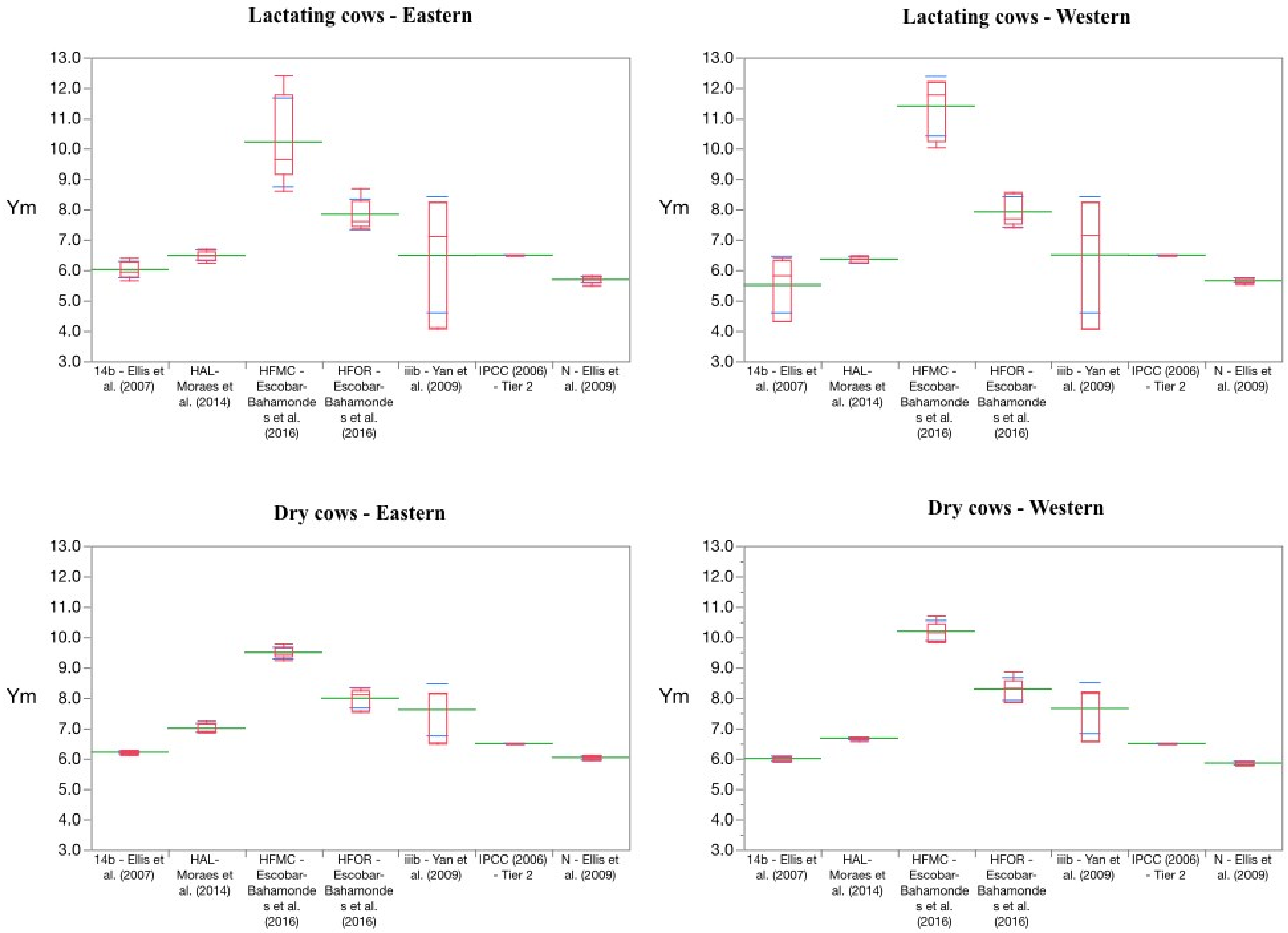
Models[a]	Eastern region			Western region		
	Average	SD[b]	CV[c]	Average	SD	CV
Lactating cows						
IPCC (2006) -Tier 2	248*c*	18.7	7.54	257*c*	9.6	3.74
14b - Ellis et al. (2007)	220*c*	21.7	9.86	209*de*	37.4	17.89
N - Ellis et al. (2009)	208*c*	11.6	5.58	214*e*	5.2	2.43
HFMC - Escobar-Bahamondes et al. (2016b)	376*a*	77.3	20.56	432*a*	44.7	10.35
HFOR - Escobar-Bahamondes et al. (2016b)	287*b*	33.2	1.11	300*b*	21.5	7.17
HAL - Moraes et al. (2014)	237*c*	13.2	5.57	241*d*	6.9	2.86
iiib - Yan et al. (2009)	235*bc*	65.0	27.66	246*bcde*	71.2	28.94
Dry cows						
IPCC (2006) -Tier 2	220*b*	16.7	7.59	250*c*	9.9	3.96
14b - Ellis et al. (2007)	195*cd*	10.7	5.49	214*e*	6.2	2.90
N - Ellis et al. (2009)	190*d*	9.8	5.16	209*f*	6.1	2.92
HFMC - Escobar-Bahamondes et al. (2016b)	299*a*	23.4	7.83	364*a*	25.1	6.90
HFOR - Escobar-Bahamondes et al. (2016b)	252*b*	25.4	10.08	296*b*	21.9	7.40
HAL - Moraes et al. (2014)	220*b*	9.3	4.23	238*d*	6.8	2.86
iiib - Yan et al. (2009)	241*bcd*	39.6	16.43	273*bcd*	31.4	11.50

Note: [a] Within a column, models with different letters differ ($P \leq 0.05$).

[b] Standard deviation.

[c] Coefficient of variation (%).

The Ym values were slightly less variable for a given equation for dry versus lactating cows (Figure 4.2) because DMI and contents of NDF, ADF, starch and GE of dry cow diets were less variable than for lactating cow diets (Table Supplementary 4.1). Some models such as iiib and HFOR were sensitive to these changes, and Ym within production phase varied for those models due to changes in nutrient intake.



Lactating cows - Eastern

Lactating cows - Western

Dry cows - Eastern

Dry cows - Western

Figure 4.2. Predicted Ym (% GEI) by different models for lactating and dry cows for Eastern and Western Canada. Long line represents the mean, line within the box plot represents the median value and the lines at the extreme of the box represent standard deviation.

4.3.3. Comparisons of predictions for growing steers

There was no difference (*P* > 0.05) in the overall mean Ym between Eastern and Western regions for growing steers during backgrounding (mean, 6.5% ± 0.99), grazing (mean, 6.6% ± 1.34) and finishing (mean, 4.8% ± 0.86; Table 4.2). However, average CH_4 production differed between Eastern and Western regions during backgrounding (116 vs. 148 g d^{-1}; $P \leq 0.05$) and grazing (209 vs. 232 g d^{-1}; $P \leq 0.05$), with no differences between regions for finishing (mean, 155 g d^{-1}; $P = 0.38$).

Differences in prediction of CH_4 production during backgrounding and grazing phases, despite no difference in Ym, indicates that these differences arose mainly due to differences in DMI. Because average daily gain differed in the previous stage, steers in the West than the East (424 vs. 384 kg), resulting in increased DMI and greater CH_4 production. The models failed to detect differences in Ym values between regions during the finishing phase even though Western steers consumed barley diets rather than corn diets, finished one month earlier than Eastern steers and had lower average DMI (9.5 vs. 10.0 kg d^{-1}, respectively) for the period.

4.3.3.1. Backgrounding in confinement.

Models differed in predicted Ym in both Eastern (4.5 to 8.2%) and Western (5.2 to 8.3%) Canada (Table 4.5). In the East, all models differed from IPCC (6.5%) with greater Ym values for iiib (8.2%), 14b (7.3%) and HFOR (6.9%) and lower values for N (6.1%), SAL (6.0%) and HFMC (4.5%). In the West, 14 b (6.6%) and HFOR (6.5%) were similar to, while iiib (8.3%), N (6.0%), SAL (5.9%) and HFMC (5.2%) were less than IPCC. The CV indicated that HFMC was highly sensitive to monthly changes in inputs, while 14b was variable in the East but not in the West with the opposite for HFOR. Similar to IPCC, iiib was not sensitive to changes in nutrient intakes over the growing period.

When calculated as CH_4 production, estimates ranged from 80 to 145 g d^{-1} in the East and from 119 to 188 g d^{-1} in the West (Table 4.6). Differences were detected among models in both locations. In the East, predictions from 14b and HFOR (128 and 122 g d^{-1}) were similar to IPCC (121 g d^{-1}, $P > 0.05$), while those from N, HFMC, SAL and iiib (107, 80, 106 and 145 g d^{-1}; $P \leq 0.05$) differed from IPCC. In the West, all predictions differed from IPCC. Emissions were generally more variable in the East compared with the West during the backgrounding phase, as indicated by the larger CV (4.5 to 15.4% vs. 1.67 to 8.4%; Table 4.6). The variability was greatest for HFMC (East and West) and SAL (East).

An important difference between regions was the source of feed; corn grain and corn silage were used in the East and barley grain and barley silage were used in the West (Table Supplementary 4.2). Steers in the West consumed more fiber and less NFC than steers in the East, which is usually associated with greater CH_4 production However, when the CH_4 response was expressed as Ym, differences in feed source were not captured by the models. Similarly, Beauchemin and McGinn (2005) reported no differences in Ym values for backgrounded steers fed corn silage or barley silage based diets, although Ym values were numerically greater for corn (7.55%) than barley diets (7.28%). While in our study overall predicted Ym values were similar in both regions (Table 4.2), some models performed differently between the two regions because they (HFMC, HFOR, 14b and SAL) use dietary components and/or BW as inputs to estimate CH_4. These models were more sensitive to changes in dietary components and/or BW inputs and hence showed more variability. In contrast, other models such as iiib, which consider GEI, DE and ME, showed less variability (Table 4.5, Figure 4.3).

Most studies that have measured CH_4 production of beef cattle used high-forage diets, although many studies evaluated feed additives or ingredients (e.g., lipids, nitrate, tannins, enzymes, organic acids, vegetable oils and meals, distillers dried grains) as mitigation strategies. In studies that used diets similar to those used in Eastern Canada, CH_4 production ranged from 105 (Staerfl et al. 2012; corn silage and concentrate; mean BW, 304 kg) to 170 g d^{-1} (Beauchemin and McGinn 2005; corn silage and corn grain; mean BW, 328 kg), and Ym from 5.1 to 5.9%, similar to values predicted by average models in our study. Studies with diets representative of those fed in Western Canada reported values from 99 g d^{-1} (Beauchemin et al. 2007; barley silage; mean BW, 222 kg) to 221 g d^{-1} (McGinn et al. 2009; barley silage; mean BW, 381 kg), with Ym ranging from 5.5 to 7.1%.

Table 4.5. Ym (% GEI) predicted from different models considering growth phase and region for growing beef steers.

Models[a]	Eastern region			Western region		
	Average	SD[b]	CV[c]	Average	SD	CV
Backgrounding phase						
IPCC 2006	6.5*c*	0.00	0.00	6.5*b*	0.00	0.00
14b - Ellis et al. (2007)	7.3*b*	0.23	3.15	6.6*b*	0.06	0.91
N - Ellis et al. (2009)	6.1*d*	0.12	1.97	6.0*c*	0.04	0.67
HFMC - Escobar-Bahamondes et al. (2016b)	4.5*d*	0.35	7.78	5.2*d*	0.29	5.58
HFOR - Escobar-Bahamondes et al. (2016b)	6.9*b*	0.04	0.58	6.5*b*	0.19	2.92
SAL - Moraes et al. (2014)	6.0*d*	0.14	2.33	5.9*c*	0.15	2.54
iiib - Yan et al. (2009)	8.2*ab*	0.05	0.61	8.3*a*	0.01	0.12
Grazing phase						
IPCC 2006	6.5*b*	0.00	0.00	6.5*b*	0.00	0.00
14b - Ellis et al. (2007)	6.4*bc*	0.47	7.34	6.7*b*	0.81	12.09
N - Ellis et al. (2009)	5.9*c*	0.12	2.03	5.8*d*	0.04	0.69
HFMC - Escobar-Bahamondes et al. (2016b)	9.1*a*	0.46	5.05	8.9*a*	0.50	5.62
HFOR - Escobar-Bahamondes et al. (2016b)	6.7*b*	0.47	7.01	7.3*b*	0.36	4.93
SAL - Moraes et al. (2014)	6.0*c*	0.03	0.50	5.9*d*	0.04	0.68
iiib - Yan et al. (2009)	5.8*bc*	1.61	27.76	4.4*e*	1.07	24.32
Finishing phase						
IPCC 2006	3.0*f*	0.00	0.00	3.0*e*	0.00	0.00
LFMC - Escobar-Bahamondes et al. (2016b)	4.1*e*	0.20	4.88	4.4*d*	0.18	4.09
LFOR - Escobar-Bahamondes et al. (2016b)	4.4*de*	0.14	3.18	5.0*d*	0.21	4.20
9b - Ellis et al. (2009)	4.6*d*	0.04	0.87	4.4*d*	0.02	0.45

A - Ellis et al. (2009)	4.9*c*	0.10	2.04	4.9*c*	0.05	1.02
I - Ellis et al. (2009)	5.1*c*	0.12	2.35	4.5*c*	0.08	1.78
SDL - Moraes et al. (2014)	5.8*a*	0.03	0.52	5.8*a*	0.02	0.34
SGEL - Moraes et al. (2014)	5.8*a*	0.03	0.52	5.8*a*	0.02	0.34
GEI - Ricci et al. (2013)	5.5*b*	0.18	3.27	5.4*b*	0.10	1.85

Note: [a] Within a column, models with different letters differ ($P \leq 0.05$).
[b] Standard deviation.
[c] Coefficient of variation (%).

Table 4.6. Methane (g d^{-1}) predicted from different models considering different diet type and phases in growing steers.

Models[a]	Eastern region			Western region		
	Average	SD[b]	CV[c]	Average	SD	CV
Backgrounding phase						
IPCC 2006	121*b*	9.3	7.69	157*b*	4.0	2.55
14b - Ellis et al. (2007)	128*b*	5.8	4.53	150*c*	2.5	1.67
N - Ellis et al. (2009)	107*c*	6.1	5.70	136*d*	2.6	1.91
HFMC - Escobar-Bahamondes et al. (2016b)	80*d*	12.3	15.38	119*f*	10.0	8.40
HFOR - Escobar-Bahamondes et al. (2016b)	122*b*	9.3	7.62	149*c*	8.4	5.64
SAL - Moraes et al. (2014)	106*c*	10.6	10.00	135*e*	7.0	5.19
iiib - Yan et al. (2009)	145*a*	11.8	8.14	188*a*	5.1	2.71
Grazing phase						
IPCC 2006	210*b*	23.7	11.29	242*b*	13.1	5.41
14b - Ellis et al. (2007)	198*b*	7.7	3.89	236*bc*	21.6	9.15
N - Ellis et al. (2009)	185*b*	15.4	8.32	205*cd*	8.5	4.15
HFMC - Escobar-Bahamondes et al. (2016b)	286*a*	39.2	13.71	317*a*	34.1	10.76
HFOR - Escobar-Bahamondes et al. (2016b)	212*b*	35.9	16.93	259*ab*	26.0	10.04
SAL - Moraes et al. (2014)	187*b*	20.1	10.75	207*cd*	11.5	5.56
iiib - Yan et al. (2009)	184*b*	65.5	35.60	157*d*	47.5	30.25
Finishing phase						
IPCC 2006	94*d*	7.3	7.77	100*e*	4.5	4.50
LFMC - Escobar-Bahamondes et al. (2016b)	132*c*	16.6	12.58	144*d*	12.3	8.54
LFOR - Escobar-Bahamondes et al. (2016b)	139*c*	15.3	11.01	165*bc*	14.4	8.73
9b - Ellis et al. (2009)	145*c*	10.0	6.90	147*d*	5.9	4.01

A - Ellis et al. (2009)	155*bc*	8.8	5.68	162*c*	5.9	3.64
I - Ellis et al. (2009)	162*abc*	8.7	8.70	146*d*	3.9	2.67
SDL - Moraes et al. (2014)	184*a*	13.1	7.12	190*a*	7.9	4.16
SGEL - Moraes et al. (2014)	184*a*	13.1	7.12	190*a*	7.9	4.16
GEI - Ricci et al. (2013)	174*ab*	7.7	4.43	178*b*	4.7	2.64

Note: [a] Within a column, models with different letters differ ($P \le 0.05$).

[b] Standard deviation.

[c] Coefficient of variation (%).

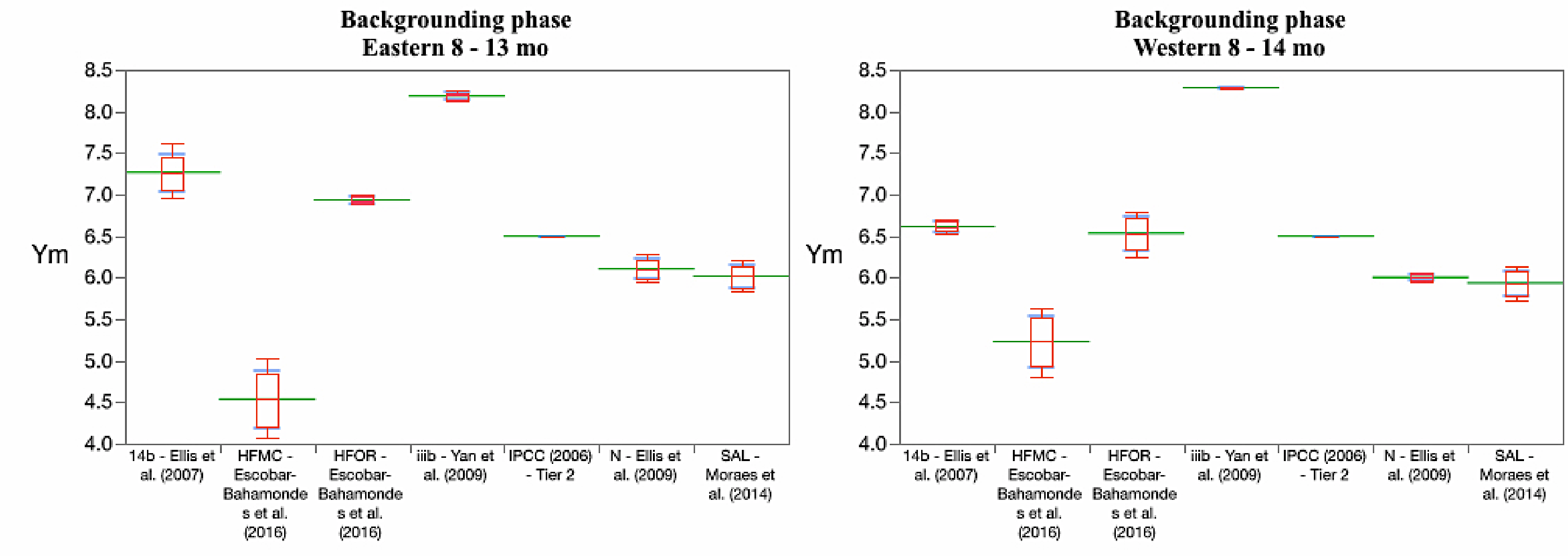


Figure 4.3. Predicted Ym (% GEI) by different models for steers backgrounded in confinement for Eastern and Western Canada. Long line represents the mean, line within the box plot represent the median value and the lines at the extremes of the box represent the standard deviation.

4.3.3.2.Grazing phase.

The main differences between regions during the grazing phase were the time the cattle remained on pasture (5 mo in East, 4 mo in West) and initial and final BW of steers (Table 4.2). In the East, the Ym for models HFOR (6.7%), 14b (6.4%) and iiib (5.8%) were similar ($P > 0.05$) to IPCC, while HFMC (9.1%), SAL (6.0%) and N (5.9%) differed ($P \leq 0.05$) from IPCC (6.5; Table 4.5). In the East, HFOR (7.3%) and 14b (6.7%) were similar ($P > 0.05$) to IPCC, while HFMC (8.9%), SAL (5.9%), N (5.8%) and iiib (4.4%) differed ($P \leq 0.05$).

Seasonal variation in composition and quality of pasture and changes in DMI of cattle can affect CH_4 emissions during the grazing phase (Boadi et al. 2001, Ulyatt et al. 2002). Variability in CH_4 production during the grazing season was accounted only by the models that include dietary components as predictors. The greatest variability in predicted Ym was observed for iiib (East, 27.8%; West, 24.3%) and 14b (East, 7.3%, West, 12.1%; Table 4.5). The other models were comparatively less responsive to changes during the grazing phase with CV < 7.3%. The evaluated models use different inputs associated with methanogenesis; iiib considers ratios between different types of energy, HFMC uses BW, DMI, HC and fat; HFOR uses BW, DMI, and fat; and 14b uses MEI, ADF and lignin. In contrast, IPCC, N and SAL were not sensitive to change in forage composition over the grazing season. Few studies have measured CH_4 production from grazing cattle because of the difficulty of measuring CH_4 and DMI on pasture. Experiments that used diets with 100% forage, as would be the case during grazing phase, reported CH_4 emissions ranging from 89 to 222 g d^{-1} (Molano et al. 2006; mean BW, 272 kg) and 260 to 297 g d^{-1} (Fitzsimons et al. 2013; mean BW, 489 kg) were consistent with our predicted modeled values.

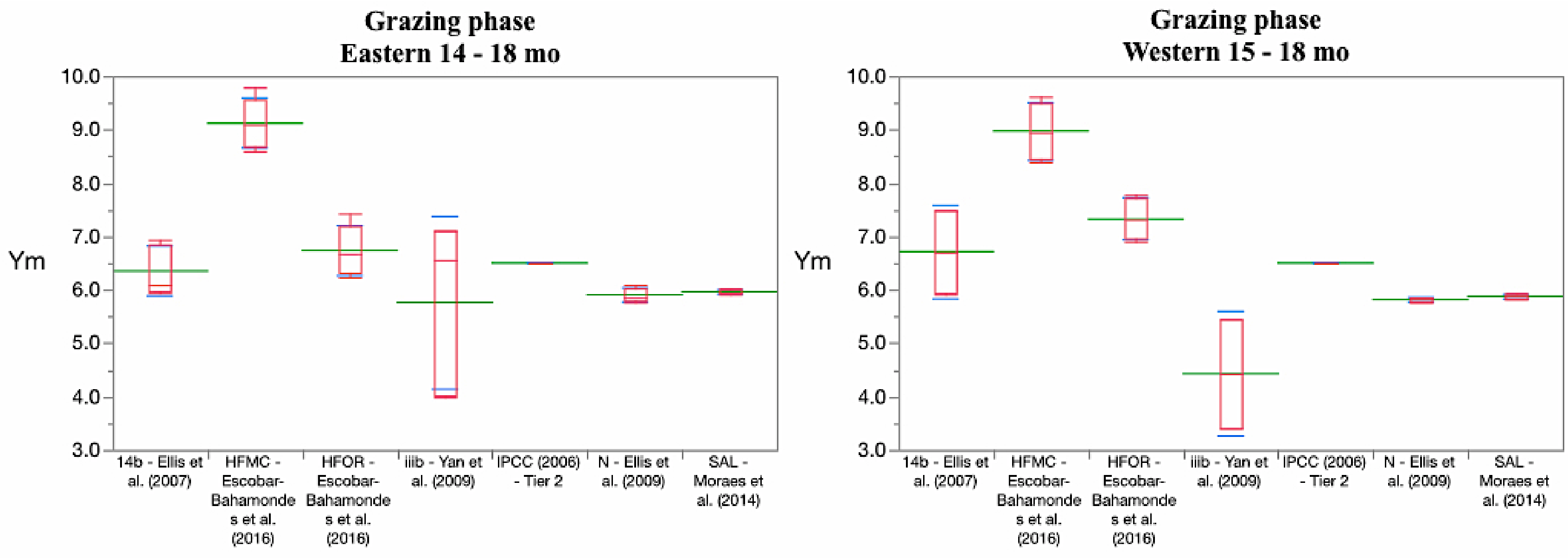


Figure 4.4. Predicted Ym (% GEI) by different models for yearling steers grazing pasture for Eastern and Western Canada. Long line represents the mean, line within the box plot represent the median value and the lines at the extremes of the box represent the standard deviation.

4.3.3.3. Finishing phase.

Despite the feeding of corn grain in Eastern Canada and barley grain in Western Canada, when averaged across models, there were surprisingly no differences in the overall average Ym (mean, 4.8%; $P > 0.05$; Table 4.2) and CH_4 predictions between the regions (mean, 155 g d^{-1}; $P > 0.05$; Table 4.2). Likewise, the variability in Eastern and Western regions for Ym (18.1 and 17.5%, respectively) and CH_4 production were similar (19.1 and 17.6%, respectively).

The Ym values for the finishing phase were lower than those obtained for cattle backgrounded in confinement or during the grazing phase. However, in both regions all models predicted greater Ym values than IPCC (Table 4.5).

Experiments that used a low proportion of forage (e.g., ≤ 10%) and barley grain similar to Western finishing diets report CH_4 production from 119 to 136 g d^{-1} with Ym of 4.0 to 5.0% (Hünerberg et al. 2013) and 101 to 116 g CH_4 d^{-1} with Ym of 4.3 to 4.5%. (Vyas et al. 2015). This range in Ym with high-grain diets is consistent with values in the current study, where the range was 4.4 to 5.8% for barley-based diets.

Beauchemin and McGinn (2005) reported a significant difference in Ym value for finishing heifers fed diets based on dry rolled corn (2.8%) as compared to steam-rolled barley grain (4.0%). Hales et al. (2012) reported a very low emission of 45.8 g CH_4 d^{-1}, equivalent to Ym of 2.4%, from steers fed a diet of mainly steam flaked corn. Lower values of Ym of finishing cattle may occur when steam flaked corn is fed due to the rapid rate of ruminal digestion of starch. However, the low Ym values obtained for steam flaked corn by Hales et al. (2012) are not consistent with values predicted for models in our study for Eastern Canada (4.1 to 5.8%) because none of the models were developed using these diet types. More recently, Vyas et al. (2014) using dry rolled corn reported values ranging from 132 to 151 g CH_4 d^{-1} equivalent to Ym of 3.9 to 4.9%, closer to the model predicted values that are reported in this study. Although the models used in the present study to predict Ym values for finishing cattle were selected from Escobar-Bahamondes et al. (2016a) to be accurate for high-grain diets, the models were not sensitive to type of grain fed.

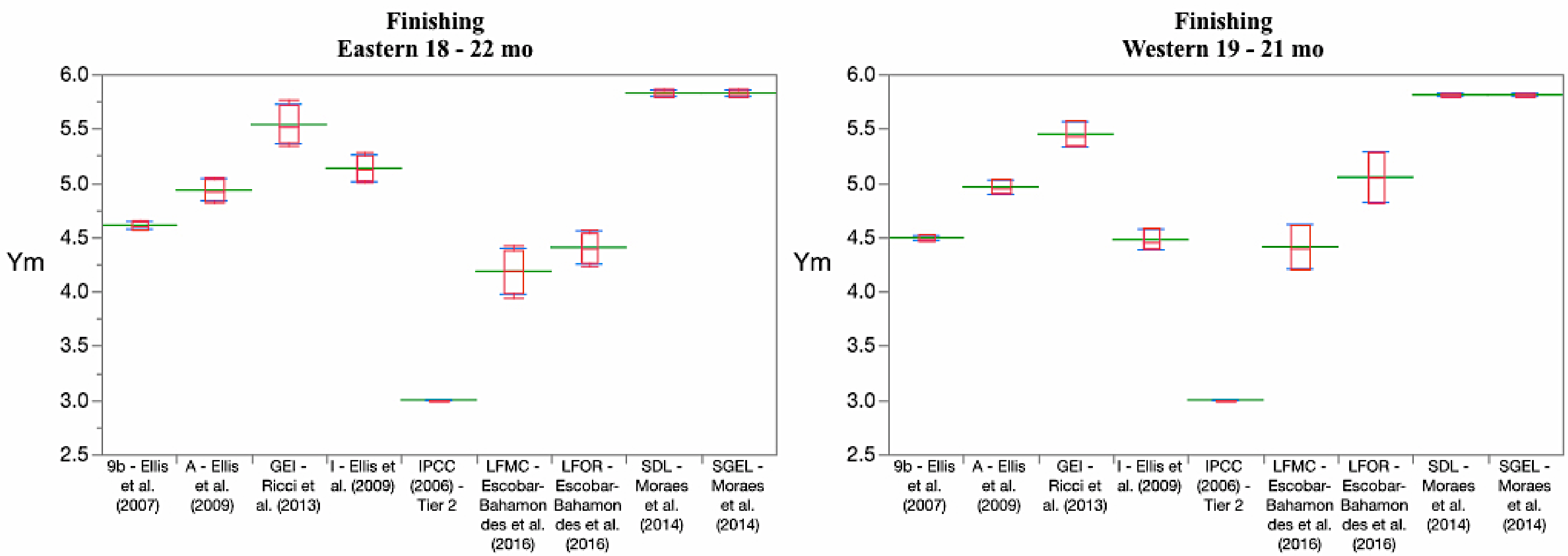


Figure 4.5. Predicted Ym (% GEI) by different models for finishing steers for Eastern and Western Canada. Long line represents the mean, line within the box plot represent the median value and the lines at the extremes of the box represent the standard deviation.

4.3.4. Model assessment and Uncertainties

Compared to the fixed CH_4 conversion factors (Ym = 6.5% for diets > 10% forage or 3.0% for diets ≥ 90% concentrate) recommended by IPCC (2006), our study showed greater variability in estimations of Ym values for beef cows and growing steers across their production cycle. The models used in the present study were those selected as best-fit for forage- and grain- based diets as well as new equations developed by Escobar-Bahamondes et al. (2016a,b). Yet, there was large variation in predicted Ym values from models ranging from 5.5 to 11.4% (mean: 8.4%) for lactating beef cows, 5.9 to 10.2% (mean: 8.0%) for dry cows, 4.5 to 8.3% (mean: 6.4%) for steers in confined backgrounding (226 to 393 kg, 8 to 12 mo), 4.4 to 9.1% (mean: 6.8%) during grazing (384 to 518 kg, 13 to 18 mo), and 3.0 to 5.8% (mean: 4.4%) for finishing cattle (564 to 708 kg, 19 to 22 mo). It is difficult to compare these estimated Ym values to observed values because of the lack of data for beef cattle in the production scenarios representative of those in Eastern and Western Canada. Thus, it is not possible to say with certainty which Ym value is most reflective of each category of cattle.

Uncertainty within models suitable for high-forage diets ranged from 0 to 45.2% (Table 4.7). Uncertainty represents the responsiveness of the model to changes in input variables (e.g., intake, diet composition), and is independent from accuracy (prediction of actual values) and precision (consistent prediction of the same value). Larger uncertainty range indicates that CH_4 production and Ym are not static throughout the production cycle in contrast to the assumption of the IPCC methodology. The range of uncertainty for Ym was smaller when variables within a particular model fluctuated minimally during the production phase of the animal. For example, use of SAL or HAL from Moraes et al. (2014) averaged across animal stages for high-forage diets had low uncertainties (2.4 and 3.4%, respectively). The SAL model considers BW and GEI, GEI increased at a constant rate with changes in BW within each phase, thus the estimation of CH_4 was consistent and uncertainty was low. In comparison, SAL and HAL models incorporate NDF (%), which changed throughout the grazing phase thereby introducing more variability in CH_4 estimation, and hence more uncertainty. Likewise, the average range of uncertainty through animal stages for high-forage diets was lower for models that used ratios between variables to adjust other variables (e.g., N from Ellis et al. 2009; 2.4%). In contrast, inclusion of more variables in models especially when inputs for these variables increased and/or decreased over time, led to greater uncertainties (e.g., HFMC from Escobar-Bahamondes et al. 2016).

In contrast to high-forage diets, low forage diets were high in energy content and nutrient contents (e.g., starch, fiber) were less variable over the finishing phase. As a result, the uncertainties of CH_4 predictions were less than for models used for high-forage diets, and ranged from 0 to 15.3%. Uncertainty was mainly affected by DMI rather than feed composition, and similar to high-forage models the uncertainty was lower for models with few variables and greater for models that use more variables.

Based on the results from our study, we suggest that when diet composition is known and data for animals are available (e.g., BW and DMI) use of complex models, as evaluated and recommended by Escobar-Bahamondes et al. (2016a,b), can achieve a high degree of accuracy when predictions of CH_4 are expressed as g d^{-1}. However in dynamic conditions the performance of the models showed more uncertainty because CH_4 production by animals varies with changes in intake and diet composition. Accuracy is decreased when CH_4 is calculated based on Ym, as is the case with IPCC Tier 2 methodology. Inversely, uncertainty of prediction is less when models only consider one variable and the range of input variables is small. However, if the purpose is to obtain estimates of CH_4 production for national inventory purposes representing cattle over a range of geographical regions where information on diet composition is lacking, use of average Ym of 6.8% is recommended for beef cattle consuming high-forage diets. An average Ym of 4.8% is recommended for finishing cattle fed high grain diets.

Table 4.7. Uncertainty of Ym for the models by production phase of mature cows (lactating and dry) and growing cattle (backgrounding, grazing, finishing)

Models	Average	Upper 95% mean[a]	Lower 95% mean[a]	Uncertainty (%)
Lactating stage				
IPCC 2006	6.5	6.5	6.5	0.0
14b - Ellis et al. (2007)	5.8	6.2	5.3	15.7
N - Ellis et al. (2009)	5.7	5.7	5.6	2.2
HFMC - Escobar-Bahamondes et al. (2016)	10.8	11.7	10.0	15.7
HFOR - Escobar-Bahamondes et al. (2016)	7.9	8.2	7.6	7.9
HAL - Moraes et al. (2014)	6.4	6.5	6.3	2.9
iiib - Yan et al. (2009)	6.5	7.7	5.3	35.9
Dry stage				
IPCC 2006	6.5	6.5	6.5	0.0
14b - Ellis et al. (2007)	6.1	6.2	6.0	2.7
N - Ellis et al. (2009)	5.9	6.0	5.9	2.4
HFMC - Escobar-Bahamondes et al. (2016)	9.8	10.1	9.6	5.8
HFOR - Escobar-Bahamondes et al. (2016)	8.1	8.4	7.9	5.9
HAL - Moraes et al. (2014)	6.8	7.0	6.7	3.8
iiib - Yan et al. (2009)	7.6	8.1	7.1	13.3
Backgrounding phase				
IPCC 2006	6.5	6.5	6.5	0.0
14b - Ellis et al. (2007)	6.9	7.2	6.7	6.9
N - Ellis et al. (2009)	6.1	6.1	6.0	2.2
HFMC - Escobar-Bahamondes et al. (2016)	4.9	5.2	4.6	12.5
HFOR - Escobar-Bahamondes et al. (2016)	6.7	6.9	6.6	4.7
SAL - Moraes et al. (2014)	6.0	6.1	5.9	3.1
iiib - Yan et al. (2009)	8.2	8.3	8.2	0.9
Grazing phase				
IPCC 2006	6.5	6.5	6.5	0.0
14b - Ellis et al. (2007)	6.5	7.0	6.0	15.6
N - Ellis et al. (2009)	5.9	5.9	5.8	2.7
HFMC - Escobar-Bahamondes et al. (2016)	9.1	9.4	8.7	8.0
HFOR - Escobar-Bahamondes et al. (2016)	7.0	7.4	6.6	11.3
SAL - Moraes et al. (2014)	5.9	6.0	5.9	1.6
iiib - Yan et al. (2009)	5.2	6.3	4.0	45.2
Finishing phase				
IPCC 2006	3.0	3.0	3.0	0.0
LFMC - Escobar-Bahamondes et al. (2016)	4.3	4.5	4.1	9.6
LFOR - Escobar-Bahamondes et al. (2016)	4.7	5.0	4.3	15.3
9b - Ellis et al. (2007)	4.6	4.6	4.5	2.8
A - Ellis et al. (2009)	4.9	5.0	4.9	3.1

I - Ellis et al. (2009)	4.9	5.2	4.5	13.9
SDL - Moraes et al. (2014)	5.8	5.8	5.8	0.9
SGEL - Moraes et al. (2014)	5.8	5.8	5.8	0.9
GEI - Ricci et al. (2013)	5.5	5.6	5.4	5.2

Note: [a] Upper and lower 95% mean indicate 95% confidence limits about the mean of model prediction.

4.4. Conclusions

There were substantial differences in predicted CH_4 production of beef cattle among models selected based on accuracy and precision. Furthermore, in most cases estimated daily CH_4 production and Ym differed from IPCC Tier 2 estimates. The variability in predicted CH_4 and Ym was greater for models that considered more dietary components as predictors. The variability due to models was greatest for grazing cattle (cows and growing steers) because of fluctuations in dietary composition (e.g., especially fibre content), intake, and BW during the productive cycle. Models that use fixed factors, such as DMI or GEI as predictors are more stable and show less uncertainty but are less sensitive to changes in diet composition that affect CH_4 production. When using IPCC (2006) Tier 2 with minimal information on diet composition a Ym of 6.8 is recommended for beef cattle consuming diets with high-forage content while a Ym value of 4.8% is recommended for finishing diets.

Supplementary Table 4.1. Ingredient intakes (DM basis) and chemical composition of the diets for beef cows in Eastern and Western Canada.

				East			
Item	Unit	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Jan-Feb
Pasture - Early season	kg d^{-1}	-	12.0	-	-	-	-
Pasture - Mid season	kg d^{-1}	-	-	10.6	-	-	-
Pasture - Late season	kg d^{-1}	-	-	-	9.3	-	-
Corn grain	kg d^{-1}	1.3	-	-	-	0.3	0.3
Alfalfa hay	kg d^{-1}	5.3	-	-	-	-	-
Orchardgrass hay	kg d^{-1}	5.3	-	-	-	10.2	10.5
DMI	kg d^{-1}	11.9	12.0	10.6	9.3	10.5	10.9
Forage content	%	88.9	100.0	100.0	100.0	97.3	91.8
OM	%	89.9	93.0	93.0	93.0	89.7	89.7
CP	%	15.9	18.2	17.1	11.2	13.6	13.6
NDF	%	45.1	58.3	53.7	60.0	56.0	56.0
ADF	%	31.5	28.4	31.5	36.8	35.8	35.8
NFC	%	26.7	13.0	19.0	18.8	17.8	17.8
HC	%	13.6	29.9	22.2	23.2	20.2	20.2
Cellulose	%	25.7	23.4	25.5	29.8	29.9	29.9
Fat	%	2.1	3.5	3.3	3.0	2.3	2.3
Sugar	%	4.1	-	-	-	0.1	0.1
Starch	%	12.5	2.5	2.5	3.0	9.0	9.0
Lignin	%	5.8	5.0	6.0	7.0	5.9	5.9
GE	MJ	18.4	20.1	19.7	19.3	18.8	18.8

West

Item	Unit	Mar-Apr	May-Jun	Jul-Aug	Sep-Oct	Nov-Dec	Jan-Feb
Pasture - Early season	kg d^{-1}	-	11.9	-	-	-	-
Pasture - Mid season	kg d^{-1}	-	-	11.6	-	-	-
Pasture - Late season	kg d^{-1}	-	-	-	11.4	-	-
Barley grain	kg d^{-1}	1.5	-	-	-	0.5	0.5
Barley silage	kg d^{-1}	-	-	-	-	-	-
Grass Legume hay	kg d^{-1}	10.9	-	-	-	-	-
Orchardgrass hay	kg d^{-1}	-	-	-	-	10.9	11.6
DMI	kg d^{-1}	12.3	11.9	11.6	11.4	11.4	12.0
Forage content	%	88.2	100.0	100.0	100.0	95.9	95.9
OM	%	89.8	93.0	93.0	93.0	89.8	89.8
CP	%	16.3	18.2	17.1	11.2	13.7	13.7
NDF	%	45.9	58.3	53.7	60.0	55.7	55.7
ADF	%	15.5	28.4	31.5	36.8	35.5	35.5
NFC	%	25.7	13.0	19.0	18.8	18.0	18.1
HC	%	30.3	29.9	22.2	23.2	20.2	20.2
Cellulose	%	9.7	23.4	25.5	29.8	29.7	29.7
Fat	%	2.0	3.5	3.3	3.0	2.3	2.3
Sugar	%	5.1	-	-	-	0.4	0.4
Starch	%	11.2	2.5	2.5	3.0	9.2	9.1
Lignin	%	5.9	5.0	6.0	7.0	5.8	5.8
GE	MJ	18.4	20.1	19.7	19.3	18.8	18.8

Note: ADF, acid detergent fiber; CEL, cellulose; CP, crude protein; DMI, dry matter intake; GE, gross energy; HC, hemicellulose; NDF, neutral detergent fiber; NFC, non-fiber carbohydrates; OM, organic matter.

Supplementary Table 4.2. Ingredient intakes (DM basis) and chemical composition of the diets for growing beef cattle in Eastern and Western Canada.

East - Steers 8 - 22 mo

Item	Unit	Backgrounder period	Grazing period	Finishing period
Pasture - Early season	kg d^{-1}	-	8.7	-
Pasture - Mid season	kg d^{-1}	-	10.2	-
Pasture - Late season	kg d^{-1}	-	11.0	-
Corn grain	kg d^{-1}	2.3	-	8.2
Corn silage	kg d^{-1}	-	-	1.0
Soybean meal	kg d^{-1}	-	-	0.4
Alfalfa hay	kg d^{-1}	1.7	-	-
Orchardgrass hay		1.7	-	-
DMI	kg d^{-1}	5.6	9.9	9.5
Forage content	%	60.0	100.0	9.9
CP	%	13.6	16.4	10.3
NDF	%	33.6	56.8	13.1
ADF	%	22.4	31.3	5.9
NFC	%	42.8	16.6	70.9
Fat	%	2.7	3.3	3.7
Starch	%	31.9	2.6	65.6
GE	MJ	18.4	19.7	18.4

West - Steers 8 - 21 mo

Feed	unit	Backgrounder period	Grazing period	Finishing period
Pasture - Early season	kg d^{-1}	-	10.7	-
Pasture - Mid season	kg d^{-1}	-	11.7	-
Pasture - Late season	kg d^{-1}	-	-	-
Barley grain	kg d^{-1}	2.9	3.0	9.0
Barley silage	kg d^{-1}	-	-	1.0
Alfalfa hay	kg d^{-1}	2.2	2.3	-
Orchardgrass hay	kg d^{-1}	2.2	2.3	-
DMI	kg d^{-1}	7.3	11.2	10.0
Forage content	%	86.7	100.0	9.5
CP	%	16.5	17.7	12.7
NDF	%	48.1	56.0	21.8
ADF	%	28.9	29.9	9.8
NFC	%	25.3	16.0	59.9
Fat	%	2.8	3.4	2.3
Starch	%	10.2	2.5	51.9
GE	MJ	19.3	20.1	18.4

Note: ADF, acid detergent fiber; CEL, cellulose; CP, crude protein; DMI, dry matter intake; GE, gross energy; HC, hemicellulose; NDF, neutral detergent fiber; NFC, non-fiber carbohydrates; OM, organic matter.

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CHAPTER 5. General discussion and final conclusion

5.1. General discussion

There are three important factors when considering CH_4 production in beef cattle production: 1) Cattle are fed two kinds of diets depending upon production stage and system, one rich in forage (cows, replacement stock, backgrounding /stocker cattle) and the other rich in grain (finishing cattle). 2) Diets rich in forage result in greater acetate and hydrogen production during fermentation in the rumen, and hence large amounts of CH_4 are produced; diets rich in grain produce more propionate than diets rich in forage, and because propionate is a major hydrogen sink less CH_4 is produced. 3) Modifications in diet composition alter the ruminal microbial population thereby changing proportions and quantities of ruminal end products including CH_4.

This thesis examined the accuracy and precision of existing empirical models that estimate enteric CH_4 production for beef cattle under different feeding conditions. These equations use dietary variables reported by commercial laboratories or those available from feed tables or estimated using mathematical relationships as model inputs. The first hypothesis of the thesis was that predicted values of enteric CH_4 production from extant equations are similar to observed values of CH_4 under different feeding conditions for beef cattle (high-forage diets: ≥ 40% forage DM; low forage diets: ≤ 20% of forage DM). Confirmation of this hypothesis would imply that no further development of prediction equations would be needed, and that any or all equations could be used with a high degree of confidence. Examination of the predictions separately for high- and low-forage diets was needed because high-forage diets have greater proportion of fiber and lower proportion of NFC promoting acetate production and methanogenesis in the rumen (Kebreab et al. 2006). McCann et al. (2014) and Fernando et al. (2010) indicate that the ruminal bacterial community is modified when diets shift from a forage:concentrate (F:C) of 60:40 to 20:80, and thus the ruminal endproducts vary depending on forage proportion in the diet. Conversely, a F:C of 20:80 or less increases amylolytic bacterial populations leading to lower CH_4 production. Thus, the first hypothesis led to the first study (Chapter 2) in which previously published models designed to estimate enteric CH_4 production were evaluated for their accuracy and precision for beef cattle fed high- and low-forage diets.

In order to evaluate the equations over a range of conditions the database was built using treatment means from published literature for beef cattle fed a wide range of diets and subsequently, a wide range in CH_4 production. The constructed database was built using scientific papers published between 2000 and 2015 for beef cattle experiments conducted around the world that reported dietary effects on CH_4 production. The data collected from the experiments were: animal descriptions (e.g. BW, breed, and gender), proportion and intakes of nutrients present in diets, type of additives and CH_4 production. Treatments using feed additives that decreased CH_4 production were then eliminated from the dataset. Previous equations were developed from unique and sometimes local databases (Ellis et al. 2007, 2009; Yan et al. 2009; Ricci et al. 2013 and Moraes et al. 2014). Consequently, these databases were limited in applicability to all classes of beef cattle or represented a limited range of diets. The range (minimum and maximum values) and distribution of each variable within the database is important because these variables are used in the equations and consequently determine the predicted CH_4 value. Upon examination of the mean and ranges of forage and dietary NDF proportions used in these databases, it was clear that in all cases the data were mostly from high-forage diets.

Tedeschi (2006) defined accuracy as: "*the model's ability to predict the right values*" and precision as "*the ability of the model to predict similar values consistently*". Chapter 2 demonstrated that equations for beef cattle lack accuracy and precision when they are used for high-forage and for low-forage diets. Selection of the best-fit equation by ranking statistics is difficult because the ranking is different according to the statistical parameter used to rank equations (i.e., equation N ranked best with respect to RMSPE, but only 5th with respect to r_c and 3rd for $R^{2adjusted}$. To overcome this limitation, one of the accomplishments of Chapter 2 was the development of a combined index using principle component analysis that considered all selection statistics to generate one unified scale that allowed equations to be ranked for overall goodness of fit.

When considering high-forage diets for beef cattle, the magnitude of the error (RMSPE) of the best equations was more than 23% (equivalent to ±35.6 g CH_4 d^{-1}), with random error (ED) as the principal source of error. The linear bias, which is an estimate of the slope of the regression between residuals and predicted values (values closer to 0 indicate that the model is unbiased), was lower for IPCC (2006) Tier 2 (0.01 g CH_4 d^{-1}) than other models (> 0.19 g CH_4 d^{-1}), indicating that IPCC had less bias in prediction than the other models. Using the combined index it was determined that, unexpectedly, the best model for estimating CH_4 in beef cattle fed high-forage diets was the model proposed by IPCC (2006) Tier 2. This model multiplies GE content (18.5 MJ kg^{-1} DM) of the diet by DMI, and indirectly represents the fraction of total fermented OM in the rumen to CH_4. However, despite being the best fit model for high-forage diets the prediction of IPCC (2006) Tier 2 was not very accurate (r_c = 0.715; RMSPE = 39.8 g CH_4 d^{-1}) and the model efficiency was only 0.56 (Chapter 2; Table 2.3).

Previous equations have tried to improve upon the IPPC Tier 2 model by including additional dietary and animal variables. Dietary variables that are positively associated with CH_4 emissions include DMI, GEI, and dietary fiber content and those negatively associated are dietary fat and starch content (Beauchemin et al. 2009; Ellis et al. 2009; Shibata et al. 2010; Moraes et al. 2014). The correlations between intakes of various dietary constituents (kg d^{-1}) were explored in detail in Chapter 3. Using high- and low-forage datasets, high correlation values were found between CH_4 and DMI (0.75, 0.79), GEI (0.67, 0.77), NDF (0.65, 0.70), or ADF (0.61, 0.61); whereas, medium or low correlation values were found between CH_4 and fat (0.28, -0.28) or starch (0.23, 0.54). Despite including additional dietary components in prediction models, the existing models lacked accuracy and precision when examined using a database representing a wide range of experimental conditions.

Low-forage diets are high in DE content because fiber components are replaced by starch, thus increasing ruminal microbial populations that promote propionate production that compete for hydrogen and decrease CH_4 production (Johnson and Johnson, 1995; Cottle et al. 2011). The best models for low-forage diets differed from those selected as best models for high-forage diets; in addition, the performance of the best models for low-forage diets was very poor. All models tested using low-forage diets had greater prediction errors than models selected for high-forage diets. On average, the magnitude of the RMSPE was 40.2% (equivalent to ±55.6 g CH_4 d^{-1}). Additionally, the overall bias was greater than models selected for high-forage diets. In the case of IPCC (2006) Tier 2, the predictions for low forage diets lacked fit and their use was undesirable for finishing cattle. A possible cause for this lack of accuracy is that most of the models tested were developed using a range of data from cattle fed high-forage diets (Ellis et al. 2007, 2009; Yan et al. 2009; Ricci et al. 2013; Moraes et al. 2014).

Because relatively few studies have developed CH_4 prediction equations specifically for beef cattle and given their modest to poor performance observed in the first study (Chapter 2) the, 2nd hypothesis was elaborated. It was hypothesized that development of new equations that better account for dietary factors and feed composition would improve the accuracy and precision of CH_4 prediction (Chapter 3). The approaches used in the second study for examining the newly developed equations were novel. Firstly, the assembled database was split according to dietary forage content into high- and low- forage datasets, such that specific equations were developed for feedlot finishing cattle and other cattle. Because measured CH_4 production data for beef cattle are limited, the statistical techniques of bootstrapping and Monte Carlo algorithms (Manly 2007) were used while keeping the same population characteristics. It was assumed that within each dataset there were subpopulations of data that shared the same properties, and that these subpopulations had similar means and distribution characteristics. These subpopulations were identified using cluster methodology and resampled by bootstrapping and Monte Carlo algorithms. However, the datasets obtained for bootstrapping were eventually eliminated beasue they failed to preserve characteristics of the original dataset. Using the original and resampled databases, new models were obtained and internally validated by cross-fold validation methodology. The new models obtained were compared with IPCC (2006) Tier 2 predictions.

The study considered normal and polynomial variables as a means of avoiding collinearity between selected variables. Although the newly developed models consider similar variables as used in other models (e.g., intakes of NDF, fat, and starch), the use of polynomial variables have additional advantages: 1) curvilinear responses are often more appropriate than linear responses, and 2) adding high-order variables (X^n) that are a function of a single variable (e.g., NDF^3) is equivalent to adding new independent variables that normally are not included together in the same model due to high collinearity (Kleinbaum et al. 1998).

The evaluation of the new models showed improvement in predictions of CH_4 production for high- and low-forage diets of beef cattle compared with IPCC (2006) Tier 2. In the case of high-forage diets, the best model was obtained from the Monte Carlo dataset with a RMSPE of 36.4 g CH_4 d^{-1}, which is less than that of IPCC (2006) Tier 2 (43 g CH_4 d^{-1}) and less that the RMSPE of 39.1 g CH_4 d^{-1} obtained from the new model generated from the untransformed dataset. The model efficiency value of 0.60 for the Monte Carlo model was closer to 1.0 compared with the other models including IPCC (2006) Tier 2 for which model efficiency was 0.51.

In the case of low-forage diets, the differences between the new models and IPCC (2006) Tier 2 were large. Again, the best fit model was obtained from the Monte Carlo dataset with a RMSPE of 12.6 g CH_4 d^{-1}, which is substantially better performance than IPCC (2006) Tier 2 (43.2 g CH_4 d^{-1}) and the model efficiency of this new model (0.86) was 1.51 points greater than the value obtained for IPCC (2006; -0.65).

The fit of the new models was better than previous models for beef cattle (e.g., Ellis et al. 2007, 2009; Yan et al. 2009; Ricci et al. 2013; Moraes et al. 2014). However, because validation of the new models was made internally using cross validation techniques it is unfair to make this comparison. A new independent database with CH_4 response to diets with right forage content (≥ 40% or ≤ 20%) would be needed to evaluate the models independently. The study clearly showed that the new models performed well when using a resampling technique and validated by cross-validation in the absence of an independent dataset. The better performance from the new equations arises from: 1) resampling of data filled the multidimensional space such that new datasets for high- and low-forage were very large (100,305 and 27,364 rows, respectively) compared with the original databases (n=123 and 34 rows, respectively) and compared with the databases used previously in other studies; 2) all relationships between variables and responses were represented with minimal loss of communalities with respect to original relationships; and 3) the stepwise regression process considered all significant variables within the model at a predetermined significance level. Newly available software (JMP© v12, SAS Institute, Cary, NC.) used in this study offered an advantage over previous methods because JMP allowed users to choose (or control) which variables will be included or excluded and to observe in real time how variables and levels of significance affect the final model. Thus, selection of variables is more interactive and more aligned with the biology of the animal.

Chapter 4 evaluated the hypothesis that using CH_4 prediction models that account for the variables of feed intake and diet composition, compared with IPCC (2006) Tier 2, may have a large effect on the estimated CH_4 production and conversion factor (**Ym**) from cattle in Canada. This hypothesis led to research to evaluate the variability among equations and IPCC (2006) Tier 2 in predicting CH_4 production (g d^{-1} and Ym) for beef cattle in Canada. The effects of the models were assessed for mature beef cows and growing-finishing beef steers using production practices that reflect typical systems used in Eastern and Western Canada. No other studies have made such comparisons of Ym or daily CH_4 production for different models for real or simulated beef cattle feeding systems. The overall results obtained from the models were within the expected range for beef cows (Ym = 5.5 - 11.4%; CH_4 production = 190 to 387 g d^{-1}) and growing cattle (Ym = 4.1- 8.3%; CH_4 production = 80 - 317 g d^{-1}) (Johnson and Johnson 1995; Beauchemin et al. 2009). However, there were large differences among models in estimated CH_4 production when expressed as g d^{-1} and Ym for beef cows and growing cattle in each region of Canada (Chapter 4; Tables 4.3, 4.4, 4.5 and 4.6).

Overall, the simulated CH_4 (Ym and g d^{-1}) for lactating cows was similar for Eastern and Western regions, when examined across all models (Chapter 4;Table 4.2). Thus differences due to diets fed in these two regions on CH_4 were not detected by the models. In contrast, there were regional differences detected during the dry period due to differences in DMI and diet composition (Legesse et al. 2016). In the case of growing steers, there was large variability among models when they were compared within phase in each region (Chapter 4; Tables 4.5, 4.6). However, the variability among models was less in Western vs. Eastern Canada, probably because of greater uniformity in DMI and chemical composition of diets (contents of fiber and NSC) over the various phases of production.

The models showed variability in predictions, with variability always lower for Ym than g CH_4 d^{-1}. The differences between model predictions expressed as g CH_4 d^{-1} reflects the fact that the models used different variables, variables with different weightings, and differences in how these variables were considered monthly.

The models evaluated in Chapter 4 can be grouped in three categories (Table 4.1): 1) linear models with two variables (Type I), 2) linear models with a large number of dietary variables alone or in combination with animal variables (Type II), and 3) polynomial models such as those developed in this thesis (Type III).

Type I models use variables (e.g. DMI, GEI) that indirectly encompass other variables (e.g. NDF, ADF, starch), thus changes in CH_4 are only due to two variables that normally do not vary extensively by month. Consequently, the CH_4 values predicted by Type I models tend to be similar to IPCC (2006) predictions, especially when the proportion of forage in diet is high. Additionally, the CV values are lower and more consistent than those of other equations. In contrast, Type III models that consider polynomial expression of dietary variables that normally exhibit monthly changes tend to generate values that are generally greater than those of IPCC (2006).

Due to monthly variations in these dietary constituents, variability of predictions is increased. Type II models result in an intermediate response between Type I and III models depending on whether the variables considered by the models change substantially over time. Comparison among models was generally similar for CH_4 expressed as g d^{-1} or as Ym, but Ym was less variable. Lower variability occurred as a result of transforming the daily emission to a percentage of GEI, which removes the variability due to intake.

With beef cows and growing cattle fed with diets containing close to 100% forage, as would be the case for yearling steers on pasture, a Ym value of 6.5% as used by IPCC (2006) seems appropriate because most models predicted Ym similar to that value. However, during the backgrounding phase where diet composition is more variable, Ym values were also more variable. For finishing cattle, all models predicted values of Ym closer to 4.0% in contrast to the value of 3.0 used by IPCC (2006) Tier 2 for diets with a high proportion of concentrate. The study suggests that IPCC (2006) Tier 2 underestimates CH_4 production of finishing cattle and that a Ym value of 4.5 to 4.8% is more suitable than 3.0% for finishing cattle. The one exception to this may be when steam flaked corn is fed, where Ym values < 3% have been reported in the literature (Hales et al. 2012). However, the equations evaluated are not able to account for the effects of grain processing on CH_4 emissions.

5.2. Future research and perspectives

Beef cattle are a source of enteric CH_4 that contributes to rising atmospheric greenhouse gas concentrations that augment climate change effects. The thesis evaluated accuracy of beef cattle enteric CH_4 prediction equations, developed new models using two different datasets that represent typical diets used in beef cattle production, and evaluated the impact of using these models on the variability of predicted CH_4 production using representative data for mature beef cows and growing-finishing beef steers in two regions of Canada.

The outcome of this research provided information that enables beef farms, advisers, environmental scientists or government agencies to choose the appropriate equations for estimating enteric CH_4 emissions from beef cattle under different dietary conditions. Based on the results from the study it is suggested that different models can be used in accordance to the level of information available for animals and diets (Table 5.1).

Table 5.1. Suggested use of CH_4 prediction models according to type of diets and amount of information available.

Data availability	High-forage diets	Low-forage diets
Scarce	IPCC (2006) Tier 2	Ricci et al. (2013) GEI
	Escobar-Bahamondes et al. (2016) HF-OR	Moraes et al. (2014) S-GEL
Detailed	Moraes et al. (2014) S-AL	Ellis et al. (2009) I
	Escobar-Bahamondes et al. (2016) HF-MC	Escobar-Bahamondes et al. (2016) LF-MC

This study helps bridge the gap in knowledge between cattle nutrition and environment using modeling techniques. Future research is needed in the short and long term to improve CH_4 prediction.

5.2.1 Short term

a) As new data become available in the literature, an independent database could be assembled and used to evaluate the new models developed in this thesis alongside with previous models for beef cattle fed a range of diets under different experimental conditions.

b) Dietary forage content affects the type of microbial population and leads to variable CH_4 production. However, with the exception of finishing diets the range of forage proportion in beef cattle diets is wide (20 to 100%). This wide range could be split in two categories to develop models for intermediate forage to concentrate ratios.

c) From a mathematical point of view, the challenge in animal nutrition is to convert typical linear cause-effect relationships identified in traditional animal feeding experiments to non-linear and multivariate analysis. A non-linear analysis would enable a better representation of processes among variables and would enable the design and construction of mechanistic models.

5.2.2. Long term

a) Models need to be tested with independent data, which represent current animal types and diets used in beef cattle production. Unfortunately the availability of data for CH_4 production from beef cattle is limited, especially data that represent diets with low forage content (finishing diets). For that reason, more research is required in the finishing phase of beef cattle.

b) The information used was collected from multiple experiments that reported information about diet composition and CH_4 production. However, variation in techniques used among laboratory groups would have contributed to variability in input values used in the models. In addition, studies differed in the manner in which CH_4 was expressed requiring conversion to a common unit (g d^{-1}), which opens the possibility of making systematic errors. One way to overcome both problems is to design a framework that involves constructing an on-line database, in which users could directly enter their individual data from experiments providing detailed data for animals, diets, environmental conditions and animal responses that would then provide information about the response variability. Also, these data could be expressed in common units and corrected according to error level that each laboratory reported in its analysis. This would provide the modeling community and researchers in animal nutrition with a tremendous resource of information and would result in widely applicable analyses available to all interested parties.

c) According to Dumas et al. (2008), calculus can be used in biology in a wide variety of applications because it can be used to describe numerically dynamic processes across time. Use of dynamic models in CH_4 prediction would better describe the process whereby feed is fermented in the rumen resulting in end products of digestion including the CH_4 formation and a complete understand of hydrogen flow in the rumen. However, the challenge with this approach is the lack of detailed information at the farm level on intakes, feed composition, and rates of digestion and passage from the rumen.

5.3. Final conclusion

Current extant models used to predict CH_4 emissions for beef cattle may give inaccurate values of CH_4 production when used arbitrarily. Selection of appropriate models for high- and low-forage diets can improve predictions.

Development of new empirical models based on forage proportion resulted in greater precision for estimating CH_4 production from beef cattle compared with IPCC (2006) Tier 2. These high- and low-forage models are simple to implement as they use variables commonly reported for beef cattle feeds by commercial laboratories. However, even when using the appropriate model, quality primary data for feed intake and diet composition are needed to generate accurate estimates of CH_4 production.

There was substantial variability in predicting CH_4 production (g d^{-1} and Ym) within each model (when animal and diets differed in a cycle productive periods) and among models (for the same animal and dietary conditions at the same time), even though the models were selected based on their accuracy for beef cattle fed high- and low-forage diets. The fluctuations in dietary composition (e.g., especially fibre content), intake, and BW during the productive cycle of mature cows and growing cattle led to variability of CH_4 production. Models that use single variables, such as DMI or GEI as predictors are more stable and less sensitive to changes in diets and physiological stage of mature cows and growing cattle. Finally, the use of an inappropriate model may introduce substantial error into CH_4 emission prediction and hence can lead to incorrect computation of greenhouse gas inventories or inappropriate mitigation recommendations.

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