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Comparing Logistic and Michaelis-Menten Multiphasic Models for Analysis of *in vitro* Gas Production Profiles of some Starchy Feedstuffs

Research Article

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ABSTRACT

Two multi-phasic models (logistic (LOG) and Michaelis-Menten (MM)) with three sub-curves were used to describe gas production kinetics of corn (CG), barley (BG), wheat (WG) and triticale (TG) grains. In each model sub curve, 1 describes the gas production caused by fermentation of the soluble fraction, gas production caused by fermentation of the non-soluble fraction is described in sub curve 2 and sub curve 3 represents gas production by microbial turnover. With MM model TG and WG had highest gas production from the soluble fraction followed by BG and CG. With LOG model there was no difference in gas production from the soluble fraction between BG and CG ($P>0.05$) and TG and WG ($P>0.05$) but TG and WG had higher gas volume from this fraction comparing to CG and BG ($P<0.05$). For gas production caused by fermentation of the non-soluble fraction, CG had the highest volume using MM model and CG and BG had higher volume with LOG model comparing to WG and TG ($P<0.05$). With MM model BG had highest gas production by microbial turnover but with LOG model WG and TG had higher gas production for the third sub curve. The LOG model had a slightly better fitting performance comparing to MM model in the present study but considering the methodology of this trial and the nature of models it does not necessarily represent the superiority of LOG model over MM model.

KEY WORDS cereals, gas production, multi-phasic models.

INTRODUCTION

A high correlation was reported between digestibility measured *in vivo* and predicted from an *in vitro* rumen gas production technique for the first time in mid-19th (Menke *et al.* 1979). Since then a considerable amount of research has used *in vitro* rumen gas techniques to predict digestibility of feeds and assess the kinetics of fermentation of various feeds for ruminants (Rymer *et al.* 2005). *In vitro* rumen gas techniques are a favorable technique because the kinetics of fermentation can be studied with this method on a single and relatively small amount of sample. They are also less time-consuming, laborious and expensive compared to *in vivo* methods. The sequence of processes that take place following the incubation of feedstuff with buffered rumen fluid has been described in some early publications (Demeyer, 1981; Hillman *et al.* 1993; Van Milgen *et al.* 1993). Upon incubation, substrates are partly solubilized. The soluble components are rapidly fermentable after incubation. A gradual shift subsequently occurs towards the fermentation of the insoluble parts, which need to be hydrated and colonized by rumen microorganisms before they can be fermented (Van Milgen *et al.* 1993). Mathematical description of gas production profiles allows analysis of data and comparison of substrates or fermentation environment characteristics and can provide useful information concerning the substrate composition and the fermentability of soluble and slowly fermentable components of the sub-

strate (Groot *et al.* 1996). More recent studies also have confirmed that fast and slow fermenting substrates which represent soluble and insoluble parts of feedstuff have different fermentation patterns, *in vitro* gas production kinetics and result in different volatile fatty acid profiles (Piquer *et al.* 2009; Cone and Becker, 2012). Multiphasic models are useful tools for assessing the kinetics of fermentation of various feeds for ruminants and can provide valuable information concerning the substrate composition and the fermentability of soluble and slowly fermentable components of the substrate. The aim of this paper was to determine fermentation kinetics of starchy feeds using two different multiphasic models. These equations will enable us to distinguish gas production kinetics of different fractions of feedstuff as well as the gas production fractional rates of each fraction.

MATERIALS AND METHODS

Sample collection and preparation

Samples of barley (BG), corn (CG), triticale (TG) and wheat (WG) grains were obtained from cooperatives located in Khorasan province, Iran. Once in the laboratory, samples were ground up and frozen (-20 ˚C) until analysis. A part of each frozen sample was oven-dried (at 70 ˚C for 48 h) and ground to pass through a 1 mm for the *in vitro* gas production analysis. The chemical composition of test feeds is presented in Table 1. Soluble washout fraction (SWF) of test feeds were determined using combined fractionation method as described by (Azarfar *et al.* 2009). To fractionate the whole grain, 5.5 g of feed sample was weighed into a pre-weighed nylon bag. The bag was placed in a polypropylene centrifuge tube, distilled water was added to reach a dilution of 20 mL water/g feed and the tube was shaken at 150 rpm for 1 h in a shaking bath. The nylon bag was subsequently removed from the centrifuge tube and rinsed on the outside with a small quantity of distilled water. The tube was then centrifuged at 715 × g for 20 min in a Beckman 2-21 M centrifuge (Fullerton, USA). After centrifugation, the supernatant was filtered through a Whatman filter paper no.541 (Whatman Corp., Springfield Mill, Maidstone, England). The resulting water, assumed to be the SWF, was decanted into a pre-weighed aluminum container and freeze-dried to determine the size of the SWF.

Gas production procedure

For the gas production procedure, rumen inoculum was collected from three ruminally fistulated steers (580±4.5 kg, body weight) prior to offering the morning feeding. Animals were fed 10.4 kg dry matter (DM), a diet containing alfalfa hay (50%), wheat straw (20%), barley grain (15%), soybean meal (14%) and mineral-vitamin premix (1%).

The ruminal content was immediately blended and strained through four layers of cheesecloth to eliminate large feed particles and transferred to the laboratory in a pre-warmed thermos. A sample of 250 mg was weighed into 125 mL serum bottles in 3 runs and 4 replicates. The filtrate was then mixed with carbonate buffer (containing ammonium bicarbonate at 4 g/L) and sodium bicarbonate (35 g/L in N-rich incubation medium and only sodium bicarbonate at 39.25 g/L in N-low medium), macro-mineral solution (5.7 g anhydrous Na_2HPO_4, 6.2 g anhydrous KH_2PO_4 and 0.6 g $MgSO_4 \cdot 7H_2O$ per liter), and deionized water in a ratio of 1:1:0.5:1.5 and 0.1 mL micro-mineral solution (13.2 g $CaCl_2 \cdot 2H_2O$, 10.0 g $MnCl_2 \cdot 4H_2O$, 1 g $CoCl_2 \cdot 6H_2O$ and 8.0 g $FeCl_3 \cdot 6H_2O$ per 100 mL) was added. The medium was then reduced by addition of 41.7 mL reducing agent (40 Ml deionized water, 1 mL 1N NaOH and 1 g$Na_2S \cdot 9H_2O$) per liter.

Twenty milliliters of medium were dispensed into a 125 mL glass serum bottle whose top was stopped with rubber and aluminum caps and placed in a 39 ˚C water bath for 72 h. Blank samples were also incubated simultaneously to make a correction in gas production, if any, from the medium. Rumen liquor was handled under a constant stream of CO_2 and all containers used were pre-warmed at 39 ˚C and filled with CO_2. Gas production was measured at 2, 4, 6, 8, 10, 12, 24, 48 and 72 h of the incubation by inserting a 23 gauge (0.6 mm) needle attached to a pressure transducer (model PX4200- 015GI, Omega Engineering, Inc., Laval, Que., Canada) connected to a visual display (Data Track, Christchurch, UK) into the headspace of serum bottles. The transducer was then removed leaving the needle in place to permit venting.

Pressure values were corrected for the amount of substrate organic matter (OM) incubated and the gas released from negative controls. In order to prevent accumulation of produced gases, the gas in the headspace of each bottle was released at each measuring.

Models and curve-fitting

In order to describe and interpret the fermentation kinetics of samples, two models were tested: The three pool Michaelis-Menten (MM) model (Groot *et al.* 1996) and three pool logistic (LOG) model, (Schofield *et al.* 1994; Pell *et al.* 1998).

These models were fitted to the cumulative gas production (individual measurements) after subtraction of gas which accumulated in the correspondent control culture.
The Michaelis-Menten (MM) model can be described as:#

$$G = \sum_{i=1}^{3} \frac{Ai}{1 + \frac{Ri^{Ci}}{t^{Ci}}}$$

In this equation, G (mL) denotes the amount of gas produced per gram of feed sample incubated at time t after incubation. Ai (mL) represents the asymptotic gas production. Ri (h) is the time after incubation at which half of the asymptotic amount of gas has been formed, and Ci is a constant determining the sharpness of the switching characteristic of the profile. The value of i indicates the number of phases in the profile (i=1, 3). The curvature is determined by B and C, resulting in a high flexibility. Curvature C determines the position of the point of inflection. Further characterization of the gas production profile is possible by estimating the maximum rate of gas production (Θ) and the time at which this maximum rate (TR) is reached (Yang *et al.* 2005):

$$TR = C\left[\frac{B-1}{B+1}\right]^{1/B} \quad \Theta = AC^{R}R\frac{TR^{-B-1}}{\left[1+C^{B}\times TR^{-B}\right]^{2}}$$

The logistic models can be described as:

$$G = \sum_{i=1}^{3}\frac{Ai}{\left[1+e^{(2+4(Ri\times t))}\right]}$$

Where:
G: cumulative volume of produced gas at time t (h).
A (mL): maximum gas production.
Θ: specific gas production rate.
t: time (h).

The value of i indicates the number of phases in the profile (i=1, 3).

In each model, sub-curves 1 to 3 describe the gas production caused by fermentation of the water-soluble fraction, non-soluble fraction and gas production by microbial turnover after exhaustion of the substrate respectively (Cone *et al.* 1997).

Goodness of fit of the models and statistical analysis

Coefficient of determination (R^2) was obtained by analyzing the data of gas volume from 2 to 96 h with NLREG (Sherrod, 2005). Root mean square prediction error (rMSPE) is an indicator of overall deviation between the observed and predicted values and can be calculated as:

$$rMSPE = \sqrt{\sum_{i=1}^{n}\frac{(V_{Pi}-V_{Oi})^2}{n}}$$

Where:
VPi and VOi: predicted and observed gas volumes respectively.
n: number of data points defining each individual curve.

The MSPE is divided into three components resulting from bias, slope and random variation around the regression line (Bibby and Toutenburg, 1977; Dhanoa *et al.* 1999), which are calculated as:

$$\begin{cases} \text{mean bias} = (\bar{V}_P - \bar{V}_O)^2 \\ \text{slope} = (SV_P - rSV_O)^2 \\ \text{random} = (1-r^2)SV_O^2 \end{cases}$$

Where:
V_P and V_O: average predicted and observed gas volumes, respectively.
SV_P and SV_O: standard deviations of predicted and observed gas volumes, respectively.
r: calculated as:

$$r = \frac{1}{n}\sum_{i=1}^{n}\frac{(V_{Oi}-\bar{V}_O)(V_{Pi}-\bar{V}_P)}{SV_O SV_{OP}}$$

Both models were fitted by using SAS (8.2) package program NLIN command and Levenberg Marquardt algorithm (SAS, 2001).

In vitro gas production parameters were analyzed using the general linear models (GLM) procedure of SAS (2001). Data were analyzed within a completely randomized experimental design. Treatment means were separated using Duncan multiple range test at 0.05 probability level.

RESULTS AND DISCUSSION

First sub curve

Gas production parameters of test feed fitted to the MM and LOG models are presented in Tables 2 and 3. With MM model WG and TG had higher gas production for the first sub curve followed by BG and CG while the rate of gas production in this sub curve was higher for BG comparing to other test feeds and there was no significant difference between WG, TG and CG.

Estimations for this parameter were slightly higher for all test feeds with LOG model comparing to MM model which is accompanied by a lower rate of gas production with LOG in comparison with MM. With LOG model WG and TG had higher gas production compared to BG and CG while the rate of gas production from soluble fraction was highest for BG followed by WG and TG and CG had the lowest rate of gas production in first sub curve. Gas production volumes caused by fermentation of the soluble fraction are in accordance with the proportion of SWF in test feeds (Table 1).

Table 1 Chemical composition and DM fractions (g/kg DM) of barley, corn, wheat and triticale grains (Mean±Sd)

Variables	Barley	Corn	Wheat	Triticale
DM (g/kg)	894±11	878±7	874±9	882±10
CP (g/kg DM)	112±3	91±2	123±3	103±2
EE (g/kg DM)	17±3	34±2	17±2	12±1
Ash (g/kg DM)	24±4	17±3	21±4	24±4
NDF (g/kg DM)	215±4	112±6	154±7	118±5
ADF (g/kg DM)	54±6	34±6	21±8	33±5
NFC (g/kg DM)	632±13	746±11	685±15	743±10
SWF	71±3	52±2	84±1	79±3
WF	224±5	170±4	231±2	215±4

DM: dry matter; CP: crude protein; EE: ether extract; NDF: neutral detergent fiber; ADF: acid detergent fiber; NFC: none fiber carbohydrate; SWF: soluble washout fraction and WF: washout fraction.

The values for A1 and Θ1 parameters for test feeds with both models were consistent with those obtained by Cone and Becker (2012) except for parameters A1 and Θ1 for WG and TG with LOG model. The higher rate of gas production in sub curve 1 comparing to sub curve 2 can be related to the chemical composition of SWF. There is very little starch and almost no neutral detergent fiber (NDF) insoluble fraction of starchy grains and this fraction mostly consists of protein, sugars and residual nonstarch polysaccharides (Yang *et al.* 2005; Azarfar *et al.* 2009). This latter fraction is probably oligosaccharides or water-soluble nonstarch polysaccharides containing β-glucans, at least in barley (Chesson, 2000).

Results of fitting *in vitro* gas production data (72 h incubation) to a biphasic model showed that gas production caused by fermentation of the soluble fraction, from CG was lower than that for BG and there was no difference between BG and WG (Cone and Becker, 2012). Relatively low gas production in the early phase of fermentation for CG has been reported by other researchers. In an *in vitro* study with a total incubation time of 72 hours using a biphasic model, asymptotic gas production for CG was significantly lower in the first sub curve comparing to peas and faba beans and was numerically lower than BG (112 *vs.* 126.5 mL) (Azarfar, 2007).

Also in agreement with our results, Azarfar *et al.* (2009) reported that following a 72 h incubation of SWF extracted from BG had higher cumulative gas volume comparing to SWF extracted from CG. In contradiction with present data, in the latter study, the maximum rate of gas production was higher for SWF extracted from CG comparing to that of BG.

Second sub curve

With MM model gas production caused by fermentation of the non-soluble fraction for CG was higher than other test feeds while with LOG model BG and CG had higher gas production than WG and TG. The rate of gas production fitting data to both models resulted in lower value for CG and differences among other test feeds were not significant.

Our results are in agreement with Yang *et al.* (2005) who reported that following 48 h incubation, the maximum rate of degradation was considerably higher for BG than for CG. The insoluble fraction in starchy feedstuff mostly consists of starch and NDF and most probably represents the fermentation characteristics of starch in samples due to the high proportion of starch in this fraction (Azarfar *et al.* 2009). Our results are in agreement with previous researchers that reported slower degradation of CG starch comparing to other starch feedstuff such as WG and BG (Hindle *et al.* 2005; Lanzas *et al.* 2007).

Differences in starch properties among different test feed can cause different fermentation patterns and it has been reported that starch in BG is more rapidly fermented than starch from CG (Nocek and Tamminga, 1991). Differences in both starch granules and the protein matrix can affect degradability of cereal (Fellner *et al.* 2008; Lopes *et al.* 2009). Proteins associated with starch granules are naturally located both within and on the surface of starch granules and they can be divided into two types: (1) endosperm storage proteins (mainly prolamins), primarily surface localized on the exterior of starch granule, and (2) starch granule-associated proteins which are distinctly different from storage proteins and are surface and / or intragranular (Baldwin, 2001). Prolamins are the major endosperm storage proteins in most feed grains and have a major effect on starch digestion. For each feed grain, they have specific and historical names: wheat (gliadin), barley (hordein), rye (secalin), corn (zein), sorghum (kafirin), and oats (avenin) (Shewry and Halford, 2002). The greater resistance to proteolytic attack of CG starch granules compared with wheat and barley starch granules may explain why CG starch is more resistant than WG or BG starch to fermentation (McAllister *et al.* 1990). The fact that several of the predominant amylolytic bacteria also possess a high proteolytic activity represents an evolutionary adaptation which is vital for the efficient fermentation of cereal grains (Giuberti *et al.* 2014). As mentioned earlier all the NDF content of starchy feedstuff remains in non-soluble fraction after extraction of SWF (Azarfar *et al.* 2009).

For insoluble components, associated with the cell-wall fraction of substrates, the rate of gas production is more likely to be affected when either chemical or structural barriers are encountered. Structural barriers to digestion and fiber characteristics depend on the plant anatomy of samples (Cornu *et al.* 1994; Agbagla-Dohnani *et al.* 2012; Cao *et al.* 2015). These characteristics are related to factors such as plant species, stage of maturity and chemical pretreatment (Lynd *et al.* 2002; Boon *et al.* 2005) and different chemical structure can even affect bacterial attachment as a primary stage in fiber digestion (Huws *et al.* 2014).

Third sub curve

For the MM model, BG had higher gas production than other test feeds with almost the same rate of gas production for all test feeds (Table 2). With LOG model TG and WG had higher gas production compared to BG and CG and there was no significant difference between the rate of gas production (Table 3). It has been reported that fast fermenting substrates cause higher amounts of microbial protein in the rumen than more slowly fermenting substrates (Cone and Becker, 2012). With the LOG model, TG and WG which had higher gas production in the first sub curve also had higher gas production in the third sub curve as a result of higher amounts of microbial protein from the fermentation of fast fermenting substrates. More likely this phase is due to turnover and fermentation of the microbial population (Theodorou *et al.* 1995; Cone *et al.* 1997).

In an *in vitro* trial Cone *et al.* (1997), reported that microbial protein in incubation bottles increased up to 10 h of incubation, coinciding with the moment all glucose was fermented and decreased upon prolonged incubation. In that trial, the NH_3 concentration inversely followed the concentration of microbial protein. This pattern most likely represents the microbial turnover. Gas production from microbial turnover complicates the interpretation of cumulative gas production profiles.

Using the gas production technique, the gas production profiles are corrected for a blank to correct for gas production in rumen fluid without the addition of a sample. Rumen fluid might contain some fermentable organic matter, disturbing the interpretation of the gas production data. However, gas production in the blank may not only be caused by fermentation of organic matter but can also be caused by turnover of the microbial population, which will start as soon as the organic matter is fermented (Cone *et al.* 1997). Correction for gas production in blanks after the exhaustion of fermentable substrates can be a source of bias because microbial turnover in does not proceed simultaneously in the blank and in the samples. Correcting for total blank gas production means that the gas production in the blank caused by microbial turnover is subtracted from gas production by the sample caused by fermentation of mainly the soluble fraction and partly the non-soluble fraction.

Table 2 Gas production parameters of test feeds fitted to the Michaelis-Menten (MM) model

Parameter	Test feeds				SEM
	Barley grain	Corn grain	Wheat grain	Triticale grain	
A1	52.21^{b}	37.91^{c}	70.92^{a}	74.34^{a}	2.10
Θ1	0.48^{a}	0.4^{b}	0.35^{bc}	0.31^{c}	0.02
A2	211.13^{b}	263.92^{a}	208.11^{b}	196.33^{b}	10.2
Θ2	0.09^{a}	0.04^{b}	0.08^{a}	0.08^{a}	0.02
A3	38.12^{a}	19.73^{b}	21.24^{b}	20.31^{b}	1.10
Θ3	0.04	0.04	0.05	0.04	0.01

A1: gas production (mL) caused by fermentation of the soluble fraction; A2: gas production (mL) caused by fermentation of the non-soluble fraction; A3: gas production by microbial turnover after exhaustion of the substrate and Θ1, Θ2 and Θ3: maximum rate of gas production (mLh^{-1}) for each phase.

SEM: standard error of the means.

Table 3 Gas production parameters of test feeds fitted to the logistic (LOG) model

Parameter	Test feeds				SEM
	Barley grain	Corn grain	Wheat grain	Triticale grain	
A1	61.63^{b}	58.81^{b}	107.72^{a}	103.23^{a}	12.1
Θ1	0.29^{a}	0.18^{c}	0.24^{b}	0.23^{b}	0.02
A2	187.34^{a}	198.82^{a}	112.12^{b}	107.23^{b}	11.7
Θ2	0.08^{a}	0.05^{b}	0.09^{a}	0.10^{a}	0.01
A3	40.33^{b}	38.82^{b}	78.41^{a}	80.01^{a}	7.1
Θ3	0.04	0.01	0.02	0.02	0.02

A1: gas production (mL) caused by fermentation of the soluble fraction; A2: gas production (mL) caused by fermentation of the non-soluble fraction; A3: gas production by microbial turnover after exhaustion of the substrate and Θ1, Θ2 and Θ3: maximum rate of gas production (mLh^{-1}) for each phase.

SEM: standard error of the means.

Table 4 Summary of root mean squared prediction error (rMSPE) and components of MSPE after fitting models

Test feeds	Multiphasic model									
	Logestic					Michaelis-Menten				
	rMSPE	Bias	Slope	Random	R^2	rMSPE	Bias	Slope	Random	R^2
Barley grain	23.96	5.2	16.20	141.10	0.96	40.65	4.1	12.20	164.5	0.89
Triticale grain	24.56	4.37	13.90	121.70	0.97	37.69	3.7	10.91	138.7	0.94
Corn grain	21.59	3.2	17.98	170.50	0.95	37.88	13.6	15.32	215.8	0.89
Wheat grain	22.47	3.7	17.41	157.30	0.96	38.52	5.8	11.76	154.6	0.90

Based on this reasoning Cone *et al.* (1997) suggested that no correction for a blank is probably better than correcting for a blank since only a very small part of the gas production in the blank is caused by fermentation of organic matter.

Statistical performance of models

Summary of root mean squared prediction error (rMSPE) and components of MSPE after fitting models are presented in Table 4. The mean square prediction error comprises errors in central tendency, errors due to regression and errors due to uncontrolled disturbance. Errors in central tendency are also known as mean bias and similarly, errors due to regression are known as slope or systematic bias (Bibby and Toutenburg, 1977). The LOG model is classic growth function and has been first employed for modeling *in vitro* gas production multiphasically by Schofield *et al.* (1994). The MM model was developed for enzyme kinetics and first employed in describing *in vitro* gas production kinetics by Groot *et al.* (1996). Residual mean square of prediction was lower and coefficient of determination was higher for all test feeds with LOG comparing to MM model. Also, predictions with MM model showed lower errors in central tendency, errors due to regression comparing to LOG except for CG that had higher mean bias with MM model. Multi phasic models have been reported previously to present acceptable goodness of fit to the cumulative gas production (Wang *et al.* 2011; Peripolli *et al.* 2014). Different studies reported superior (Calabrò *et al.* 2005; Huhtanen *et al.* 2008) to moderate fit (Dhanoa *et al.* 2000) for MM model. In our study, the MM had lower goodness-of-fit comparing to LOG model and higher model-predicted asymptotic gas volumes which is consistent with Huhtanen *et al.* (2008). It has been reported previously that prolonged incubation times (Huhtanen *et al.* 2008) and increasing numbers of data points (Calabrò *et al.* 2005) might favor the fit performance of the MM model. It should be noted that although LOG model showed slightly better fitting performance in present study, Dhanoa *et al.* (2000) and Huhtanen *et al.* (2008) indicated that the LOG model was not necessarily a good alternative because the main constraints of LOG model in fitting raw gas data were fixed inflexion points and positive intercepts at 't= 0'.

CONCLUSION

Both models can describe the *in vitro* gas production of starchy feedstuff with three pools and results are consistent with the nature of test feeds and literature. The LOG model had a slightly better fitting performance comparing to MM model in the present study but considering the methodology of this trial and the nature of models it does not necessarily represent the superiority of LOG model over MM model.

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