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New bicompartmental model: an application for the production of gases using the *in vitro* technique

Novo modelo bicompartimental: uma aplicação para a produção de gases pela técnica *in vitro*

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Highlights

New model that can generate more accurate estimates.
Possibility of a new model perform better in terms of parameter convergence.
New model performed better than published model.

Abstract

The purpose of this study was to propose a bicompartmental nonlinear model and to identify the best-performing model between the proposed model and the bicompartmental logistic (BL) mode regarding the quality of fit to the curve of cumulative gas production (CGP) using corn silage, sunflower, and their mixtures. Gas production was measured 2, 3, 4, 6, 8, 9, 10, 12, 15, 19, 24, 30, 36, 48, 72, and 96 h after beginning the *in vitro* fermentation process. The generated data were used to generate the parameters of each model tested using the *stats* package of the R computational tool version 4.0.4. The mathematical models were subjected to the following selection criteria: the adjusted coefficient of determination ($R^2_{aj.}$), residual mean square (RMS), mean absolute deviation (MAD), and Akaike information criterion (AIC). It was demonstrated that the proposed model had better performance with a high $R^2_{aj.}$, and lower values of RMS, AIC, and MAD than the bicompartmental logistic model for the prediction of the parameters of cumulative

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gas production (CGP), per to present a superior fit in the set of criteria according to the methodology and conditions in which the present study was developed.

Key words: Corn silage. Mathematical models. Proposed model. Ruminal kinetics. Sunflower silage.

Resumo

No presente trabalho, com silagem de milho, girassol e suas misturas, objetivou-se propor um modelo não linear bicompartimental e identificar entre o modelo proposto e Logístico Bicompartimental (LB), aquele que apresenta maior qualidade de ajuste à curva de cinética de produção cumulativa de gases (PCG). A leitura da produção de gás foi realizada nos tempos 2, 3, 4, 6, 8, 9, 10, 12, 15, 19, 24, 30, 36, 48, 72 e 96 horas, após o início do processo de fermentação *in vitro.* Os dados gerados foram utilizados para geração dos parâmetros de cada modelo testado com auxílio do pacote *stats* da ferramenta computacional R versão 4.0.4. Os modelos matemáticos foram submetidos aos seguintes critérios de seleção o coeficiente de determinação ajustado ($R^2_{aj.}$), quadrado médio do resíduo (QMR), desvio médio absoluto (DMA) e o critério de informação de Akaike (AIC). Foi demonstrado que o modelo proposto teve melhor desempenho com altos $R^2_{aj.}$, e menores valores de QMR, AIC e DMA, por apresentar um ajustamento superior no conjunto dos critérios em comparação com o modelo logístico bicompartimental para a predição dos parâmetros de produção cumulativa de gases (PCG) de acordo com a metodologia e condições em que foi desenvolvido o presente estudo.

Palavras-chave: Cinética ruminal. Modelos matemáticos. Modelo proposto. Silagem de milho. Silagem de girassol.

Introduction

Ruminal digestion is one of the most important and relevant processes for utilizing nutrients in the diet. The *in vitro* gas production technique allows the direct measurement of the ruminal digestion rate associated with gas production and the respective gravimetric measurement of the diet or feed under testing (Assis et al., 2021).

Nonlinear mathematical models that adequately describe the parameters involved in the kinetics of ruminal digestion were selected for use because they provide a simple interpretation of the phenomena studied through a few parameters of easy biological interpretation (Emiliano et al., 2014).

Several nonlinear unicompartmental and bicompartmental models have been proposed and evaluated for different substrates and treatments (Wang et al., 2011; Velho et al., 2014; Cabral et al., 2019). The bicompartmental logistics (BL) model provided a better fit for the gas production curve. However, the most appropriate evaluation model depends on the type of diet or food consumed (Assis et al., 2021).

Recently, mathematical models have been proposed to better describe the cumulative gas production (CGP) data (Santos et al., 2019, 2020). Thus, there is always the possibility that a new model may perform better in terms of biological convergence and interpretation of parameters (Santos et al., 2021). In addition, few studies have been conducted on the kinetics of ruminal degradation of corn or sunflower silage as the only roughage in the diet or its associations.

Therefore, this study aimed to propose a bicompartmental model and compare it with the BL model to identify the model that presents the highest quality of fit to the CGP curves produced using corn silage and sunflower and its mixtures.

Materials and Methods

Data used

This study was conducted at the Nutrition Laboratory of the Animal Science Department of the Veterinary School of the Federal University of Minas Gerais (UFMG). The evaluation of the gas production kinetics of four experimental diets was carried out. These diets met the animals' requirements, according to the National Research Council [NRC] (2001). The diets contained increasing proportions of sunflower silage in place of corn silage as roughage: Treatment 1 - corn silage as a single roughage plus concentrate (100SM); Treatment 2 - forage composed of 66% corn silage and 34% sunflower silage, plus concentrate (340SG); Treatment 3 - roughage composed of 34% corn silage and 66% sunflower silage, plus concentrate (660SG), Treatment 4 - sunflower silage as single roughage, plus concentrate (100SG) (Tables 1 and 2).

Table 1
Chemical composition and fermentation parameters of corn and sunflower silages

Items (g kg^{-1} of DM)a	Corn Silage	Sunflower silage
DM (g kg^{-1} de NM)	300.0	272.0
CP	69.0	88.0
NDF	569.0	493.0
ADF	332.0	373.0
EE	38.0	126.0
Ca	1.8	12.2
P	1.6	10.0
pH	3,97	4,56
N-NH$_3$ (% do total de N)	6.05	16.86

DM: dry matter; NM: natural matter; CP: crude protein; NDF: neutral detergent fiber; ADF: acid detergent fiber; EE: ethereal extract; Ca: calcium; P: phosphor; N-NH3: ammonia nitrogen; N: nitrogen

Table 2
Chemical composition of experimental diets based on dry matter

Items (g kg^{-1} of DM)	SM	340SG	660SG	SG
DM	369.0	372.0	365.0	367.0
CP	161.0	161.0	168.0	165.0
NDF	477.0	456.0	441.0	428.0
ADF	265.0	278.0	275.0	299.0
NFC	287.0	272.0	267.0	253.0
EE	27.0	44.0	59.0	74.0
Ca	6.0	6.3	6.3	6.2
P	4.4	4.4	4.5	4.6

DM: dry matter; CP: crude protein; NDF: neutral detergent fiber; ADF: acid detergent fiber; NFC: non-fibrous carbohydrates; EE: ethereal extract; Ca: calcium; P: phosphor; SM: 1000 g kg^{-1} of corn silage; 340SG: 340 g kg^{-1} of sunflower silage and 660 g kg^{-1} of corn silage; 660SG: 660 g kg-1 of sunflower silage 340 g kg-1 of corn silage; SG:1000 g kg^{-1} sunflower silage with $NFC\% = 100\% - [CP\% + (NDF\% - NDCP\%) + EE\% + Ash\%]$.

Four fistulated Holstein cows (multiparous, weighing approximately 550 kg, with an average daily production of 25 kg of milk per animal and between 60 and 82 days of lactation) were used. In the laboratory phase, *in vitro* incubation was carried out in glass flasks with a capacity of 160 mL, which were washed with distilled water and dried.

Subsequently, two flasks were used per treatment, that is, two for each cow in each of the four treatments and two more blank flasks (containing only culture medium and inoculum) per inoculum. The culture medium consisted of a mixture of buffer solution, macrominerals, resazurin, and reducing agents, prepared according to the recommendations of Theodorou et al. (1994).

Proposed model - applied mathematical models

Recently, Santos et al. (2019) presented growth and degrowth construction methods based on a combination of existing models. Among those listed by the authors, we used the growth and degrowth model construction method via combinations of the weighted sum of models power or linear combinations of existing power models (see equation (2), p. 3).

Thus, the proposed model developed in this study resulted from the combination of the unicompartmental models of Orskov and Mcdonald (1979) and a logistic model (Schofield et al., 1994), denoted using OML, combining Equations (1) and (2) as follows:

$$W_I(t) = \alpha_1 \{1 - exp[-k_1 t]\} + \varepsilon \qquad (1)$$

$$W_{II}(t) = \alpha_2 \{1 + exp[2 - 4k_2(t - \lambda)]\}^{-1} + \varepsilon \qquad (2)$$

Therefore:

$$\alpha_1 \{1 - exp[-k_1 t]\} + \alpha_2 \{1 + exp[2 - 4k_2(t - \lambda)]\}^{-1} + \varepsilon \; (3)$$

In addition to the proposed model, we used the BL model, as it is most commonly used in the area to adjust the *in vitro* gas production of diets and feed for ruminants. According to Peretti et al. (2017), several researchers have used the BL model proposed by Schofield et al. (1994) for kinetic studies on cumulative gas production. Therefore, the bicompartmental model proposed by (Schofield et al., 1994) was used, which was adjusted to the cumulative gas production curves given by

$$\alpha_1 \{1 + exp\,[2 - 4k_1\,(t - \lambda)]\}^{-1} + \alpha_2 \{1 + exp\,[2 - 4k_2\,(t - \lambda)]\}^{-1} \quad (4)$$

In these models: W(t) is the accumulated gas volume (mL) at time t; α_1 is the maximum volume of gases produced from the rapid digestion fraction of non-fibrous carbohydrates (NFC) mL/g; α_2 is the maximum volume of gases produced from the slow digestion fraction of fibrous carbohydrates (FC) mL/g; k_1 is the rate of degradation of the rapid digestion fraction (NFC) h^{-1}; k_2 is the degradation rate of the slow digestion fraction (FC) %..h^{-1}; λ, bacterial colonization time (h); *t*, the fermentation time; e, exponential; and ε is the random error associated with each observation with normal distribution, zero mean, and constant variance.

The estimates of the nonlinear models' kinetic parameters were obtained through the method of least squares using the iterative Gaussian Newton process and the *Nonlinear Least Squares* (nls) function of the Stats package. This was performed using the free software R version 4.0.4 (R Development Core Team, 2021).

Residues

Most existing studies on the fitting of nonlinear growth curve models ignore statistical tests. Therefore, the Shapiro–Wilk test was used to verify the normality assumption, the Durbin–Watson test to verify independence, and the Breusch–Pagan test to verify the homoscedasticity of the residues.

Criteria for model selection

The criteria used to select the model that best described the growth curve were the adjusted coefficient of determination ($R^2_{aj.}$), residual mean square (RMS), Akaike information criterion (*AIC*), and mean absolute deviation (MAD), defined as follows:

$$R^2_{aj.} = 1 - \frac{(1 - R^2)(n - 1)}{n - p}$$

$$RMS = \frac{\sum_{i=1}^{n} |y_i - \hat{y}_i|}{n}$$

$$AIC = n + n\,log\,log\,(2pi) + n\,log\,log\left(\frac{RSS}{n}\right) + 2(p + 1)$$

$$MAD = \frac{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2}{n - p}$$

where R^2 is the coefficient of determination; y_i is the observed weight; $\hat{y}_i$ is the estimated weight; *n* is the number of observations; *p* is the number of parameters; and RSS is the residual sum of squares. All statistical procedures were performed using R software.

Results and Discussion

Table 3 presents the results of the residue analysis for the models fitted to the gas data of sunflower and corn silages and their mixtures using the Shapiro–Wilk, Durbin–Watson, and Breusch–Pagan tests. The results of the test adjustments indicated that the assumptions of normality and homoscedasticity of errors were not violated. As for the Durbin–Watson test, the independence assumption was not satisfied; that is, there is evidence that the residuals are dependent.

These results are in agreement with those of Santos et al. (2020), who showed identical dispersion when using the BL nonlinear model to describe CGP growth using corn, sunflower silage, and their mixtures for all tests. The estimated residuals for the bicompartmental logistic-von Bertalanffy (LVB) model proposed by the authors were normally distributed, independent, and homoscedastic; that is, all assumptions about the SG treatment residues were met, while the SM, 340SG, and 660SG treatments showed normality and independence despite violating homoscedasticity.

Residual analysis plays a key role in the process of fitting a regression model; therefore, if any of these assumptions are not met, the model is insufficient, and this bias must be corrected or accounted for in the model (Fernandes et al., 2014).

Table 3
Statistical values of the Shapiro-Wilk, Durbin-Watson and Breusch-Pagan tests, with the respective p-value, applied to the residuals of the OML and BL models, adjusted to the PCG for SM, 340SG, 660Sg and SG

Treatment	Shapiro-Wilk	p-value	Durbin-Watson	p-value	Breusch-Pagan	p-value
SM_{OML}	0.9543	0.5608	1.0691	0.0089	0.4632	0.4961
SM_{LB}	0.9419	0.3730	1.1824	0.0185	0.7354	0.3911
$340SG_{OML}$	0.9293	0.2379	0.8725	0.0020	0.9453	0.3309
$340SG_{LB}$	0.9389	0.3366	1.0983	0.0109	0.3366	0.5618
$660SG_{OML}$	0.9313	0.2541	0.8716	0.0020	0.4249	0.5145
$660SG_{LB}$	0.9358	0.3014	1.1512	0.0153	0.7187	0.3966
SG_{OLM}	0.9000	0.0804	0.7919	0.0010	0.0209	0.8850
SG_{LB}	0.9145	0.1374	1.1428	0.0146	0.5289	0.4670

The estimates of the parameters of the *in vitro* kinetic degradations of non-fibrous carbohydrates and fibrous carbohydrates (Table 4) indicate that the OML model obtained the highest values for $\hat{\alpha}_1$ (103.05; 154.88; 188.02; and 195.68) and the lowest values for $\hat{\alpha}_2$ (69.59; 54.28; 54.22; and 75.87) in relation to BL, with values of $\hat{\alpha}_1$ (95.78; 109.05; 143.05; and 167.14) and $\hat{\alpha}_2$ (69.82; 88.04; 80.37; and 78.63) for SM, 340SG, 660SG and SG, respectively. The cumulative gas production is the sum of the digestion of non-fibrous and fibrous carbohydrates. The OML model yields the highest cumulative gas production at all levels. The data referring to these degradability parameters indicated that the increase in sunflower silage participation in the levels increased the total volume of gases. This observation was corroborated by Santos et al. (2020), who observed an increase in the total volume of gases caused by the sum of FC and NFC when the proportion of sunflower silage increased. Aragadvay-Yungán et al. (2015) used sunflower silage as a single forage or mixed it with corn silage at 25%, 50%, and 75% and found that corn silage had higher total gas production but lower fermentation rates than a mixture containing 25% sunflower silage.

The gas production rate $\hat{k}_1$ was lower for the OML model than for the BL for SM treatment, with 340SG, 660SG, and SG exhibiting a similar rate with values of 0.03 for the OML model and 0.02 for the BL model. The rate $\hat{k}_2$ of gas production from fibrous carbohydrates was higher for SM levels and 340SG (0.11 and 0.10), respectively, with the OML model than with the BL model (0.02 and 0.09) and lower estimated values (0.08 and 0.06) than with the BL model (0.10 and 0.09). Comparing the LVB and BL models to evaluate corn and sunflower silages and their mixtures, Santos et al. (2020) verified values of $\hat{k}_1$ and $\hat{k}_2$ similar to our study for the BL model at all levels. For the LVB model, they observed higher values of $\hat{k}_1$ (0.08, 0.07, 0.07, and 0.02) and lower $\hat{k}_2$ (0.06, 0.06, 0.06, and 0.20) for SM, 340SG, 660SG, and SG, respectively, except for the SG level.

The latency $\hat{\lambda}$ of the OML model was higher for all levels compared to the BL model. The highest latency was observed for 100% sunflower silage, with values of (7.27 and 5.79) for the (OML and BL) models, respectively. Aragadvay-Yungán et al. (2015) used sunflower silage as a single roughage or mixed it with corn silage in the following proportions: T1= 100% corn silage, T2= 75% corn silage 25% sunflower silage, T3= 50% corn silage 50% sunflower silage, T4= 25% corn silage 75% sunflower silage, and T5= 100% sunflower silage. They verified in their study that sunflower silage as a single roughage presented the highest latency, and treatments with 75% corn silage and 25% sunflower silage presented the lowest latency.

The OML model showed the highest values of $R^2_{aj.}$ (99.94, 99.90, 99.85%, and 99.87) for all treatments (SM, 340SG, 660SG, and SG, respectively), indicating that this model had the best fit (Table 4). When evaluating the RMS, AIC, and MAD, the highest values were obtained with the BL model in relation to the OML model, according to (Table 4). According to the results, the BL model is the least suitable for describing the cumulative gas production curves. Based on these criteria, the smallest deviation was observed for the OML model.

According to all the criteria adopted to verify the quality of fit for the LVB and BL models, Santos et al. (2020) also observed that their proposed model was better than BL. Evaluating several models (Exponential, France, Gompertz, Logistic, and BL) to describe the cumulative gas production curve in ruminant diets where corn was replaced by different levels of crude glycerol (0, 4, 8%, and 12%), Peripolli et al. (2014) concluded that the best model was BL. By evaluating several models, including von Bertalanffy, Logistic, BL, Logistic modified, Gompertz, Brody, and France, to describe CGP in corn and sunflower silages, Mello et al. (2008) concluded that the best model was the BL based on the following criteria: coefficient of determination, mean square of the residue, graphic analysis of observed and estimated curves, graphic analysis of dispersion of studentized residues, average percentage error, relative efficiency, and number of iterations of the models. Comparing six nonlinear mathematical models, Veira (2018) concluded that the BL model presented the best fit for most of the evaluated foods: corn straw, soybean hulls, coffee husks, souari nuthusks, citrus pulp, extruded beans, corn, dry distillery grains with solubles, corn silage, Tifton 85 silage, corn bran, wheat bran, and soybean meal, with a higher coefficient of determination and lower Bayesian Information Criterion and Euclidean distance values. Mjoun (2018) also found a better fit of the corn silage *in vitro* gas production with the BL model after comparing it with exponential, logistic, dual-pool logistic, France, Gompertz, dual-pool Gompertz, Groot, and McDonalds-Ørskov models.

Table 4

Estimated parameter values (α_1, α_2, k_1, k_2, e λ) and evaluators used in the selection of the most suitable non-linear model for the OML and BL model fitted on data from SM, 340SG, 660SG and SG

Levels	Models	Parameters					Evaluators			
		$\hat{\alpha}_1$	$\hat{\alpha}_2$	$\hat{k}_1$	$\hat{k}_2$	$\hat{\lambda}$	$R^2_{aj.}$	*MSR*	AIC	MAD
SM	OML	103.05	69.59	0.04	0.11	5.50	**99.94**	**2.88**	**68.34**	**1.20**
	BL	95.78	69.82	0.09	0.02	4.56	99.87	5.86	79.71	1.63
340SG	OML	154.88	54.28	0.03	0.10	5.94	**99.90**	**6.35**	**81.00**	**1.80**
	BL	109.05	88.04	0.02	0.09	4.62	99.80	12.93	92.36	2.51
660SG	OML	188.02	54.22	0.03	0.08	6.22	**99.85**	**12.17**	**91.39**	**2.55**
	BL	143.05	80.37	0.02	0.10	5.01	99.73	21.96	100.8	3.36
SG	OML	195.68	75.87	0.03	0.06	7.27	**99.87**	**13.48**	**93.03**	**2.73**
	BL	167.14	78.63	0.02	0.09	5.79	99.71	29.82	105.7	3.89

In Figure 1, all models fitted the gas production data well, exhibited an S-shape, and could be divided into three distinct phases: a) an initial phase characterized by low gas production, b) an exponential phase characterized by rapid gas production, and c) an asymptotic phase, in which the rate of gas production decreased and eventually reached zero. However, the OML model showed a slightly superior fit to the data. This observation corroborates the results of Santos et al. (2020), who reported that the BL model was less effective in fitting the exponential and asymptotic phases of the curve. The authors also reported that the replacement of the second-compartment logistic model with the von Bertalanffy model resulted in adjustments at all stages of the fermentation process for the LVB model. Mello et al. (2008) reported that the BL model exhibited adequate curve shapes at all stages up to 144 h post-incubation, except for a small trend at 18 h post-incubation in corn silages.

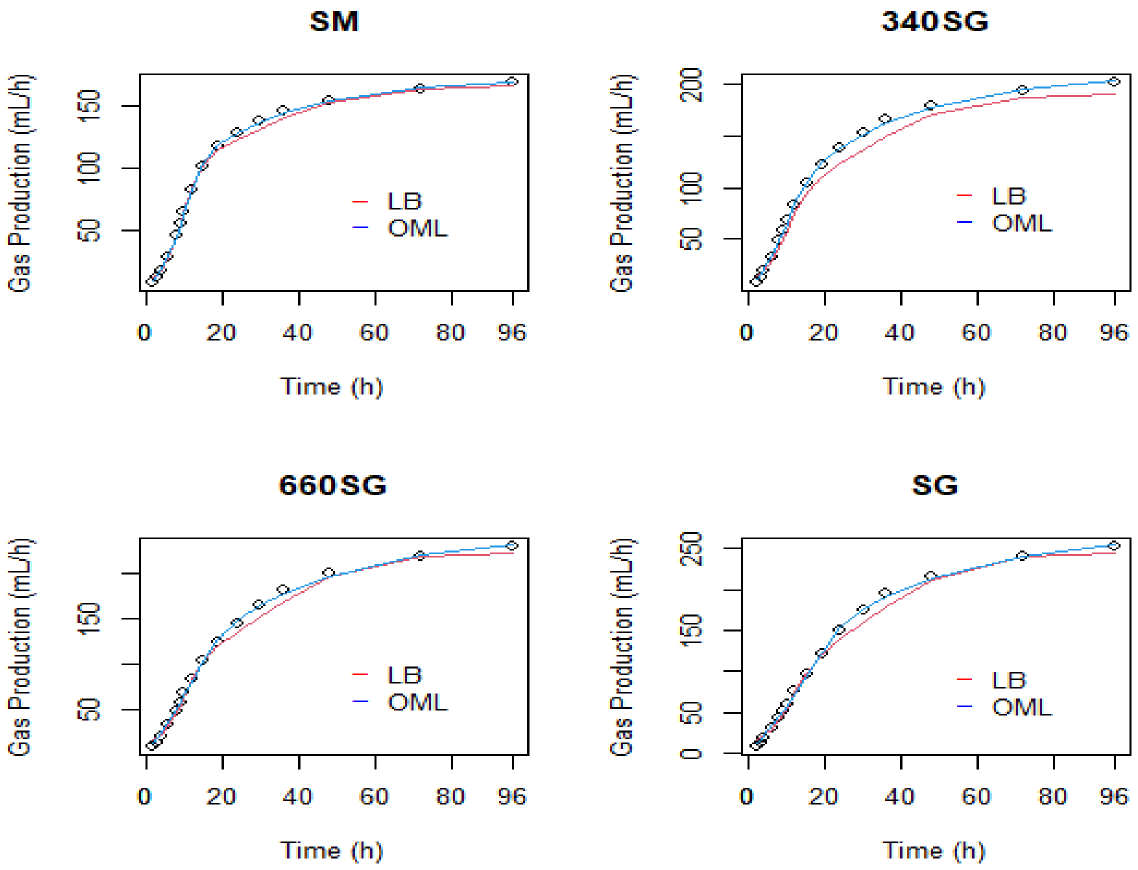

Figure 1. Cumulative gas production curves for SM, SG, 340SG and 660SG, over the incubation time, from the observed data and adjusted by the OML and BL models.

Conclusion

The OML and BL models satisfactorily described CGP growth curves in sunflower and corn silages and their mixtures, providing parameters with practical interpretations. However, the OML model presented the best fit for all the levels of in vitro gas production, allowing for more reliable parameter estimates. More comprehensive future directions for improving research include using longer degradation and incubation times, different gas measurement systems, incorporating different feeds and diets in evaluating degradation kinetics in vitro in dairy and beef cattle and validating these results in vivo. Furthermore, the OML model represents an alternative to other models and contributes to research.

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