

Scientific Electronic Archives

Issue ID: Sci. Elec. Arch. Vol. 13 (4)

April 2021

DOI: <http://dx.doi.org/10.36560/14420211317>

Article link: <https://sea.ufr.edu.br/SEA/article/view/1317>



Mathematical modeling applied to ruminal digestion and gas production *in vitro*

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Abstract. The ruminal digestion performed by ruminants is one of the essential and most important processes for the use of dietary nutrients. However, the use of mathematical models applied to digestion kinetics has been widely applied to provide prediction of animal performance, maximize the use of nutrients and reduce nutritional losses due to excreta and a reduction in the cost of animal production. In this context, it aimed to conduct a literature review on the use of mathematical models and to analyze comparisons of different models to predict ruminal digestion. The *in vitro* gas production technique provides direct measurement of the ruminal digestion rate associated with gas production and the respective gravimetric measurement of the food or diet under test. Nonlinear models are chosen to evaluate ruminal digestion due to a better interpretation of biological parameters; they produce exponential and sigmoidal growth equations. However, the most suitable model for evaluation depends on the type of food or diet. The two-compartment logistical model presents a better adjustment of the gas production curve, mainly for foods with a high proportion of fiber. Among this, single-compartment models can be well applied to evaluate the degradation kinetics of foods with low fibrous carbohydrate content. Therefore, the choice of the most appropriate model is up to the researcher to assess which model best suits the chemical-chemical composition of the food or diet.

Keywords: Ruminal kinetics, Mathematical models, Exponential and logistic equations

Introduction

The dietary systems of ruminants need information about the food, mainly about their fractions of carbohydrates and proteins, as well as their digestion rates in order to be able to more accurately predict the performance of animals and consequently maximize the efficiency of nutrient use (MOREIRA et al., 2010).

However, the kinetic parameters of degradation are important because in addition to describing digestion, they characterize the intrinsic properties of foods that limit the availability of nutrients for ruminants (Mertens, 2005). The mathematical models applied to the degradation kinetics can provide strong estimates of the nutritional values of the food, microbial population, physiological state of the animal and also information related to the factors that affect the digestive processes (MERTENS, 1993).

In this context, the variables of the kinetics of digestion of nutrients in the gastrointestinal tract, make it possible to provide more adequate diets aiming at maximum efficiency of microbial protein synthesis and also the reduction of nitrogen and energy losses resulting from the ruminal fermentation process, thus providing observations synchronization in the degradation of nitrogen and carbohydrates in the rumen environment (MERTENS, 2005).

Therefore, the objective was to conduct a review of analytical literature on the use of mathematical models in *in vitro* systems to predict rumen digestion and to analyze comparisons between models to predict ruminal digestion kinetics.

Contextualization and Analysis

Ruminal digestion

Carbohydrates are the main source of energy for microbial growth and microbial protein being the main source of essential amino acids for the host. Therefore, variations in the fractions and in the rates of degradation of these nutrients contained in food, can affect the supply of microbial protein in the small intestine and consequently animal performance (CABRAL et al., 2000). Thus, the study of the digestive kinetics of carbohydrates is of great importance, making it possible to adapt diets to synchronize the availability of energy and nitrogen compounds in the rumen, which will allow the maximum performance of microbial populations and host animals (RUSSEL et al., 1992).

The availability of nutrients for ruminants depends on the degradation carried out by ruminal microorganisms. The microbial growth in the rumen varies with the conditions of the rumen environment, such as temperature, pH, osmotic pressure, type of food and fermentation products. In this context, the ruminal degradation kinetics generates information about the digestion process, by which it can better describe the nutritional value of food (VAN SOEST, 1994). However, it allows a thorough understanding of digestive activity, obtaining a more specific value of the nutrients contained in food by measuring the production of gases resulting from the digestion process (VAN SOEST, 1994).

Therefore, digestibility measures have been valuable tools for the development of systems that define the nutritional value of foods (VAN SOEST, 1994). Bearing in mind that in order to determine the nutritional value of food, one should not rely on the results of chemical analysis alone, as these have little validity, and the biological attributes of food have greater significance for predicting animal performance, consequently for the dietary balance (Rocha Júnior et al., 2003). However, it is more difficult to determine the precise values, being explained by the fact that there is an interaction between the composition of the food and the digestive and metabolic capacity of different animals (PRESTON, 1999).

Ruminal degradation kinetics with gas production

In vitro gas production techniques were developed to predict the fermentation of food for ruminants and consequently to estimate animal performance. In this technique, the food is incubated with ruminal liquid, buffer and culture medium and the gases produced are measured as indirect indicators of ruminal fermentation kinetics. The incubated food is degraded and the degraded fraction can be fermented by ruminal microorganisms and produce gases (CO₂ and CH₄) and acids from fermentation or be incorporated into microbial biomass (RYMER et al., 2005). The main objective of the *in vitro* gas production technique is to promote relevant information in the interpretation of food nutritional values and / or animal performance and / or animal impacts on the environment (KRISHNAMOORTHY, 2005).

The cumulative production of gases as a function of time is represented graphically by three distinct phases: 1) slow phase or no gas production (initial phase); 2) the phase of rapid gas production (exponential phase); and 3) the phase in which the rate of gas production is slow and may even cease (asymptotic phase) (BEUVINK and KOGUT, 1993; Figure 1).

The kinetics of ruminal degradation and the fractional rate of *in vitro* gas production are related to the type of carbohydrates, protein profile and the content of ether extract in food. However, the synchronization of the degradation of carbohydrates and nitrogen in the rumen, enhances the maximum efficiency of microbial protein synthesis, reducing energy (CH₄) and nitrogen (NH₃) losses resulting from the rumen fermentation process, thus being able to more accurately predict the performance of the animals based on dietary ingredients (RUSSELL et al., 1992; SNIFFEN et al., 1992). In Figure 1, an example of the fermentation of different types of carbohydrates is presented on the profile of the gas production curve *in vitro*.

Since the late 1970s, the measurement of gas production *in vitro* has become increasingly popular to determine the digestion and kinetics characteristics of forage fermentation in the rumen (THEODOROU et al., 1994). Gas production is measured by digesting the forage mass (substrate) with rumen liquid buffered inside a sealed amber glass. The microorganisms present in the rumen liquid ferment the substrate, forming the final fermentation products, such as carbon dioxide (CO₂) and methane (CH₄) gases, short-chain fatty acids, mainly acetate, propionate and butyrate. However, the amount of gas produced depends on the substrate level and microbial activity, as well as on the quantity and molar proportions of the volatiles produced during the fermentation process. Thus, the gas produced during incubation is measured to predict the extent and rate of digestion of food (GETACHEW, 2004) or diets.

In vitro gas production data is strengthened when complemented with other information, such as the chemical composition of the substrate and / or digestion of the same *in vitro* (digestibility), thus being able to act in more complex mathematical models that predict phenomena related to the functioning of the ruminal environment (KRISHNAMOORTHY, 2005).

The *in vitro* gas production technique has advantages over other *in vitro* methods that are based only on the quantification of final post-fermentative residues. Because gas production can effectively predict the different digestion rates of the carbohydrate fractions in foods (fraction: A, B1 and B2). In addition, fermentation kinetics can be obtained from a large number of food samples in a single incubation (GETACHEW, 2004). However, it is important to note that another advantage is the simplicity of the method, as it does not require sophisticated equipment, facilitating the conduct of

experimental research in different animal nutrition laboratories.

The gas production method is more efficient when compared to the *in-situ* method to assess the effects of anti-nutritional factors, such as tannins. In the *in situ* method these factors are dispersed in the rumen, after being released from the nylon bag, and apparently do not affect the rumen fermentation due to the low content (MAKKAR et al., 1995). The *in vitro* gas production method better controls the interactions between nutrients and antinutritional agents (MAKKAR et al., 1995). As an example, there is the complexation between tannins and

dietary macromolecules (proteins and carbohydrates), which can cause problems with the use of the methods of Tilley and Terry (1963) and the nylon bag of Mehrez and Orskov (1977). Additionally, the last two techniques are based on gravimetric evaluation, with the quantification of residues after fermentation, providing tannin solubilization, which does not contribute to energy production (KHAZAAL et al., 1994). However, for the *in vitro* gas production technique, the effects of tannins on ruminal fermentation of food are reflected in gas production.

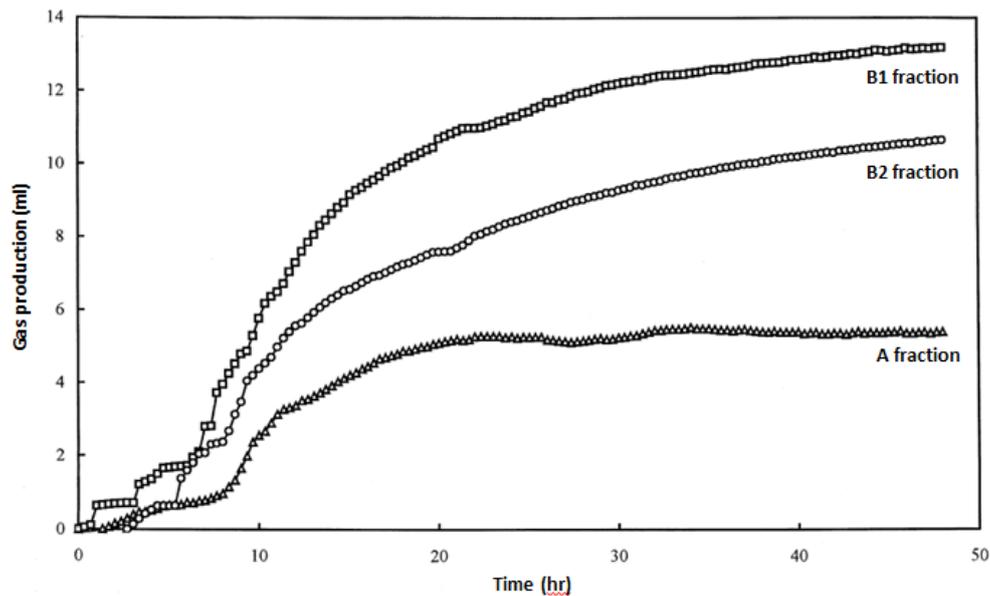


Figure 1. Gas production curves for corn silage (whole plant). Three carbohydrate fractions: fraction A (triangles) representing sugars, fermentable organic acids and short oligosaccharides; fraction B1 (squares) representing starchy and pectic substances; and a B2 fraction (circles) representing digestible fiber (Adapted from Pill et al., 1999).

However, some factors can compromise *in vitro* fermentation and influence the measurement of gas production, such as the source and preparation of the inoculum, composition and preparation of the culture medium and preparation of the substrate. Another limitation of the gas production technique is the fraction of gases from CO₂ resulting from chemical reactions with the bicarbonate contained in the culture medium (PELL et al., 1994). In addition, gas production is a reflection of rumen microbial metabolism, so studies with diets deficient in essential nutrients for microbial growth may provide misleading information.

In general, gas production data *in vitro* are useful when complemented with other information, such as the chemical composition of the substrate and / or its digestion *in vitro*, so that it can act on more complex mathematical models that predict phenomena related to the functioning of the rumen (KRISHNAMOORTHY, 2005). Therefore, the interpretation of cumulative gas production data must be cautious, requiring mathematical models that adequately interpret the degradation profiles of

each food or diet, together with the knowledge of the chemical composition of the food in terms of its *in vitro* digestibility.

Mathematical models in ruminal degradation kinetics

The rumen environment is a complex and heterogeneous system, formed by a liquid and solid digest with stratifications of these contents in different layers, which makes the digestive process in ruminants a dynamic system that involves the entry and exit of liquids, microorganisms and undigested residues (PEREIRA et al., 2005). Therefore, the mathematical modeling of productive functions, connected to mathematical programming and the empirical evaluation of predictions based on the results of digestive processes, allows a biological understanding of this complex system and provides an adequate dietary formulation aiming at better animal performance (VIEIRA et al., 2008).

Pioneering studies of mathematical modeling by compartments were carried out with the aim of translating the complexity of natural phenomena so that they can be used in prediction in

the real world. The concepts that have been established in these studies have been widely applied successfully to the nutrition of ruminants, providing a theoretical framework on the changes undergone by digestion in the gastrointestinal tract (FRANCE et al., 1985; ALLEN and MERTENS, 1988; VAN MILGEN et al., 1991; SCHOFIELD et al., 1994).

Non-linear mathematical models are chosen for application in ruminal digestion kinetics, as they provide a simple interpretation of the studied phenomena through few parameters with biological interpretation (EMILIANO et al., 2014). Several non-linear equations have already been proposed and tested for the different substrates used (FRANCE et al., 2005; MELO et al., 2008; RODRIGUES et al., 2009; UCKARDS et al., 2013; UCKARDS and EFE, 2014), each with different assumptions and treatments. These are mainly aimed at describing changes in the system as a function of the incubation time. However, models with different mathematical structures can produce different results from the same gas production curve.

Among the nonlinear models used for the mathematical description of gas production profiles, exponential and sigmoidal growth stands out. Assuming that the specific rate of gas production can be proportional to the amount of substrate and independent of the microbial mass (exponential with limited substrate); independent of the amount of substrate and proportional to the microbial mass (simple exponential with "cut-off"); or proportional to the amount of substrate and microbial mass (SCHOFIELD et al., 1994). Additionally, the models can assume one, two or more compartments and / or fermentation phases.

Brody's model is a non-sigmoidal exponential model, with three parameters that assumes the specific rate of gas production in proportion to the amount of substrate and independent of the microbial mass (exponential with limited substrate). According to Beuvink and Kogut (1993), the adjustment of the exponential model for the production of gases is inferior to the sigmoid models. However, because it is a model characterized by simple exponential growth, it may be more able to describe the production of gases after the inflection point of the initial phase of the curve or on substrates where the latency period is not evident (lag discrete time), considering zero time ($t = 0$) as an inflection point and, thus, being able to describe the entire post-incubation gas production curve (SOUZA, 2013). When readings of gas production are not frequent in the initial phase (0 to 12 hours) post-incubation, the inflection point of the curve may not be apparent, so in this case a non-sigmoid model would better describe the data (MELLO et al., 2008).

The exponential model is the non-sigmoidal model, being frequently used in the evaluation of food, using the nylon bag technique (ORSKOV and MCDONALD, 1979). This model describes simple

first order kinetics, with or without a latency phase. In the case of gas production, the rate of gas production is proportional to the amount of gas that has yet to be produced, which is a reflection of the substrate concentration. It is noteworthy that the adjustment in the exponential model for the production of gases is inferior to all other sigmoid models (BEUVINK and KOGUT, 1993).

In the logistic model it is assumed that the rate of gas production is proportional to the microbial activity, represented by the sum of gas already produced and the concentration of the substrate (BEUVINK and KOGUT, 1993). A serious problem with the linear transformation and the linear regression method in estimating the kinetic parameters is the error in estimating the indigestible fraction (MERTENS, 2005). Considering that the definition of the asymptotic phase is essential to estimate the indigestible residue, the potentially digestible fraction and the rate of fractional degradation of the fiber (MERTENS, 1977).

The Gompertz model assumes that the rate of gas production is proportional to microbial activity, but the proportionality parameter decreases over time, according to the first order kinetics, which can be attributed to the loss of efficiency in the fermentation rate with time (SCHOFIELD et al., 1994; BEUVINK and KOGUT, 1993). Logistic and Gompertz equations produce sigmoidal curves, but differ in the mathematical aspect of limiting the substrate on the rate of gas production. Bearing in mind that the same parameters in both models, where the period before a significant increase in volume, is longer in the Gompertz model, however the gas production rate rises more quickly after that long period. Additionally, the inflection point of the gas production curve occurs at the beginning with the Gompertz model (ZWIETERING et al., 1992).

In the case of the France model, it is derived from the generalized Mitscherlich equation, presenting the advantage that the specific rate of gas production can vary throughout the fermentation process (FRANCE et al., 1993). This model allows the rate of fractional degradation to remain constant, decrease or increase asymptotically over time, taking into account the dynamics of the fraction of the components of the food. Nevertheless, France model has been criticized for having parameters (b and c) in biological interpretation (FONDEVILA e BARRIOS, 2001).

Models for assessing digestion kinetics based on gas accumulation using a single pool approach (FRANCE et al., 1993) do not have full applicability. Such models may have a high predictive value for simple substrates, but they were not designed to evaluate kinetics with multi-pools. A model with a single pool tends not to show the presence of two components in a substrate, unlike the adjustment provided by models that consider different pools. In addition, the parameters used in these models lack a better biological understanding.

Table 1. Experiments comparing different mathematical models on the kinetics of ruminal degradation *in vitro* in different types of foods.

Author	Foods	Model	CP	NP	AC	IT	Animal	Conclusion
Cabral et al., 2019	Rice husk, sugar cane, cassava shavings, pupunha residue, and forage turnip residue	France Exponential Logistic Gompertz Orskov and McDonald Two-compartment exponential Two-compartment logistics	1 1 1 1 2 2	4 3 3 3 2 5 5	MB; CCC; MSPE.	72 hours	Does not declare	The bicompartmental models were the most suitable. Bicompartmental logistics for rice husks and cassava shavings. Bicompartmental exponential for sugar cane, turnip and pupunha.
Días et al., 2014	Corn, soybean meal and corn silage (whole plant)	Gompertz Logistic France Two-compartment logistics	1 1 1 2	3 3 4 5	R ² _a ; RMS; MSE.	24 hours	Does not declare	The bicompartmental logistic model showed lower values for RMS and MSE in relation to the other evaluated models, which is the model that best describes the kinetics of ruminal fermentation of corn, soybean meal and corn silage.
Velho et al., 2014	Corn silages (whole plant) at different stages of maturity	Exponential France Gompertz Logistic	1 1 1 1	3 4 3 3	RMS; MB; SRAEE; RER.	24 e 48 hours	Cattle	The Gompertz model better describes the kinetics of <i>in vitro</i> gas production in corn silages. The France model is not suitable to describe the kinetics of gas production with times less than or equal to 48 hours of incubation.
Farias et al., 2011	Babassu bran and pie	Gompertz Two-compartment logistics	1 2	3 5	RMS; R ² ; RMAS.	96 hours	Cattle	Logistic model showed lower values for RMS and RMAS and better value for RMS. The logistic model was better to describe the kinetics of ruminal fermentation of bran and babassu cake.
Mello et al., 2008	Sunflower silage	Brody Von Bertalanffy Gompertz France Logistic Modified Logistics Two-compartment logistics	1 1 1 1 1 1 2	3 3 3 4 3 3 5	R ² ; MSQE; MSE; RE.	192 hours	Does not declare	The two-compartment Logistic and France models showed higher relative efficiency, respectively, in sunflower and corn silages. Thus, the two-compartment Logistics model has a higher quality of fit to the gas production curve in sunflower and corn silages.
Azevedo, 2007	Pseudofruit of five cashew clones (CP 06, CP 09, CP 76, CP 1001 and BRS 189).	Logistic Gompertz Exponential France	1 1 1 1	3 3 3 4	MSQE; R ² ; RMAS.	72 hours	Cattle	The logistic, exponential and France models proved to be more adequate in describing the dry matter gas kinetics of cashew pseudofruit in relation to Gompertz. However, it better described the ruminal fermentation kinetics of the NDF fraction.

AC: evaluation criteria; AF: accuracy factor; BIC: bayesian information criterion; CCC: correlation coefficient of correlation; CP: compartments; DMA: desvio médio absoluto dos resíduos; ED: Euclidean distance; IT: incubation time; MB: medium bias; MSE: mean standard error; MSPE: mean square of the prediction error; MSQE: mean squared error; NDF: neutral detergent fiber; NP: number of parameters; RE: relative efficiency; RER: residual error; RMAS: residual mean absolute deviation; RMS: residual mean square; R²: determination coefficient; R²_a: adjusted coefficient of determination; SRAEE: square root of the average estimation error.

Continued Table 1.

Author	Foods	Model	CP	NP	AC	IT	Animal	Conclusion
Noguera et al., 2004	5 sorghum genotypes: Massa 3, Volumax, BR601, BR700 and BR701.	Orskov and McDonald Logistic France Gompertz	1 1 1 1	3 3 4 3	R ² ; RMS.	96 hours	Cow	The Orskov and McDonald and French models were inadequate to describe fermentation kinetics, as they underestimate the production of gas at the beginning of fermentation and in the asymptotic phase. The Gompertz model was better because it offers an appropriate adjustment in the first stages of degradation, as well as in the asymptotic phase of the curve.
Peripolli, et al., 2014	Diets replacement of corn with crude glycerol (0, 4, 8 and 12%). Bulky hay source of alfalfa 60% of the diet	Exponential France Gompertz Logistic Two-compartment logistics	1 1 1 1 2	3 4 3 3 5	R ² ; MSQE; RMAS; RE.	48 hours	Sheep	The double pool logistic model had the lowest RMAS value and relative efficiency greater than 1.0 in all comparisons and, therefore, was considered the most efficient of the evaluated models.
Veira, 2018	Pumpkin peel, coffee peel, pequi peel, soy bean peel, sweet corn co-product, DDGS corn, corn bran, soy bran, wheat bran, extruded beans, corn straw, citrus pulp, cob corn, sweet corn co-product silage, corn silage and tifton 85 silage.	Von Bertalanffy Brody France Gompertz Logistic Bicompartmental Logistics	1 1 1 1 1 1	3 3 4 3 3 5	R ² ; BIC; DE.	72 hours	Adult crossbred cattle	The France model was not effective in adjusting the gas production kinetics with lower R ² and ED. Bicompartmental logistics best suited food for corn straw, soybean husk, coffee husk, pequi husk, citrus pulp, extruded beans, corn DDGS, corn silage, tifton silage 85, corn bran, bran wheat and soybean meal with the highest R ² and the lowest BIC and ED values. The Bertalanffy model showed the best fit for corn cob food. The Brody model for foods co-produced by sweet corn and silage, with the highest R ² values and the lowest BIC and ED values. The Gompertz model better adjusted the production of gases from the pumpkin peel with higher values of R ² and lower BIC and ED.
Uckards and Efe, 2014	White clover (<i>Trifolium repens</i> L.) Red clover (<i>Trifolium pretense</i> L.) Common vetch (<i>Vicia sativa</i> L.) Yellow sweet clover (<i>Melilotus officinalis</i> L.)	Logistic Orskov Verhulst Janoscheck Weibull Bridges Mitscherling Brody Von Bertalanffy	1 1 1 1 1 1 1 1 1	3 3 3 4 4 4 3 3 3	MSQE; R ² ; AF; BIC.	96 hours	Does not declare	It is concluded that these models, except the Orskov model, can be used to estimate the kinetics of gas production <i>in vitro</i> using different forage crops.

AC: evaluation criteria; AF: accuracy factor; BIC: bayesian information criterion; CCC: correlation coefficient of correlation; CP: compartments; DMA: desvio médio absoluto dos resíduos; ED: Euclidean distance; IT: incubation time; MB: medium bias; MSE: mean standard error; MSPE: mean square of the prediction error; MSQE: mean squared error; NDF: neutral detergent fiber; NP: number of parameters; RE: relative efficiency; RER: residual error; RMAS: residual mean absolute deviation; RMS: residual mean square; R²: determination coefficient; R²_a: adjusted coefficient of determination; SRAEE: square root of the average estimation error.

Multicompartmental models consider that each substrate (phase) is digested independently. This can answer the differences in substrate accessibility due to the hydration of the particles, microbial adhesion and the increase in the number of microorganisms after the latency time. According to Doane et al. (1997), the double compartment can occur by the fermentation of heterogeneous substrates, from two different microbial populations, or by the combination of the factors involved.

When food is a heterogeneous substrate, the use of more complex mathematical models can better predict changes in the digestion kinetics of different carbohydrate fractions. For this reason Schofield et al. (1994) suggest that multicompartmental models have better fit quality than models based on first-order kinetics.

The bicompartamental logistic model has characteristics from the nutritional point of view, more relevant than the other models, since it has mathematical devices that can calculate gas production curves by the degradation of total carbohydrates and the B2 fraction of the Cornell system (fibrous carbohydrates). Proceeding with the subtraction technique, a third curve is obtained by the degradation of the A + B1 fractions of the Cornell system, composed of soluble sugars, starch and pectin (SCHOFIELD and PELL, 1995). Thus, this model divides the total gas production into two compartments distinguished by their digestion rates (fast and slow) (Figure 1).

However, several mathematical models to predict ruminal digestion *in vitro* have already been proposed, but in this section we address only the most used and those that were innovative in a historical perspective of mathematical modeling applied to *in vitro* ruminal degradation kinetics aligned with the gas production technique. Therefore, for a deeper understanding of mathematical modeling for ruminal kinetics and gas production technique, the reader is invited to the work of Lopes (2005) and Pitt et al. (1999), respectively.

Comparison of different mathematical models of ruminal kinetics

Several non-linear models with different assumptions and treatments are available to adjust the gas production curves and to determine the degradation parameters or rumen fermentation profile. The main objective of these models is to describe changes in the system as a function of the incubation time. Table 1 shows experiments evaluating different models of different types of food for ruminants.

Final considerations

Carbohydrates are the main energy fraction of the diet and generally the one that most affects the rate of ruminal digestion, and it is extremely important to adapt diets to synchronize the availability of energy and nitrogen compounds in the

rumen, consequently maximizing animal performance.

The gas production technique has been widely applied in several animal nutrition laboratories. Because it is possible to more accurately predict the rate of digestion of foods or diets based on the cumulative production of gas, together with an association of digestibility with the final post-fermentative residue.

Nonlinear models are the most requested to assess ruminal digestion, as they provide better interpretation of results through few biological parameters. In general, the main mathematical models used present exponential and sigmoidal growth equations.

However, the most suitable model for assessing ruminal degradation kinetics depends on the type of food or diet. However, the bicompartamental models in particular, the logistic one, present a better adjustment of the gas production curve, mainly for foods with a high proportion of fiber. However, to evaluate the kinetics of ruminal degradation of foods with low fibrous carbohydrate content, monocompartmental models can be used. Thus, the choice of the most appropriate model is up to the researcher to assess which model best suits the chemical-chemical composition of the food or diet.

Therefore, the use of a large number of models should not cause difficulty in deciding which model to use. Since the reaction of the model will be different depending on the food used for gas production. While a model may show better fit for a data set in one study, it may perform poorly in another study with another food. In this way, several models can be used for a study, after which it is necessary to select the model with the best fit and be more appropriate for the data set of a particular food or diet under study.

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