Revista Brasileira de Zootecnia

Evaluation of mathematical models to describe gas production kinetics of some tropical and temperate forages

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ABSTRACT - Our objective was to identify the best fit mathematical models for *in vitro* gas production kinetics using rumen fluid and forage plants commonly used in ruminant feed to obtain better estimates of parameters that describe the rumen fermentation. Four mathematical models were tested, two unicompartmental (M1 = first order, M2 = Gompertz) and two bicompartmental (M3 = M1 + M2; M4 = M2 + M2). Two temperate grasses were evaluated, as well as four tropical grasses and three temperate forage legumes. The fit of the models was verified by the corrected Akaike information criterion ($AICc_r$) and the difference among $AICc_r$ values (Δ_r), likelihood probability (W_r), and relative likelihood (ER_r). Temperate forages reached maximum gas production between 48 and 72 h. In the tropical forages, it occurred only after 72 h. In profiles in which M3 was the best choice, the values of parameters V_{f1} were higher than those of V_{f2}, and k_1 values were higher than k_2 values. The only exception was for Tifton 85 profile, whose V_{f2} value was higher than V_{f1}. The model M3 has a better fit for tropical forages with higher fiber content and lower levels of nonfibrous carbohydrates and crude protein. The model M1 has a better fit for forage with higher nonfibrous carbohydrate contents and low lignin content.

Keywords: *in vitro*, kinetic parameters, ruminal kinetics

Introduction

Degradation rate changes may happen depending on the plant and the parts that are available for degradation (Vieira et al., 2012; Abreu et al., 2014), due to the proportion and digestibility of fibrous (FC) and nonfibrous carbohydrates (NFC). These changes occur with great frequency, both with the advance of the forage cycle, as between species. The digestive process of different substrates does not occur at the same rate and, consequently, the fermentation profiles and gas production from degradation is variable. Thus, it is important to identify the degradation profile of each forage species to obtain better use of the nutrients with the appropriate adjustment of the diets, according to the degradation rates of each food.

Mathematical models that describe ruminal kinetics profile are generally sigmoid (Mertens, 1977; Van Milgen et al., 1991; Dhanoa et al., 1995), characterized by an initial delay (lag time) followed by an exponential growth that decelerates until reaching an asymptotic phase (Vieira et al., 2008). Carbohydrates from plant cell walls have a diverse nature (Van Soest, 1994); thus, Schofield et al. (1994),

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proposed a mathematical model with two compartments to describe carbohydrate degradation in the ruminoreticulum using two different degradation rates, with a common latency for both compartments. However, carbohydrate degradation profile may fit better with other mathematical models, such as those that consider only one compartment with or without the latency period, or others that consider two compartments being one with latency and the other without it.

This helps to obtain reliable estimates of each ruminal degradation rate. Still, it collaborates to determine possible effects of the plant in the mathematical model parameters estimates that describe the rumen degradation kinetics. The use mathematical models that adequately describe the parameters involved in ruminal degradation is still a challenge when compared in more detail, such as the chemical composition and degradability of the forages. Abreu et al. (2014) described that these models were built to provide means of quantifying the nutritional value of diets for ruminants and may help in predicting animal performance. Therefore, to obtain better estimates from parameters that describe ruminal fermentation, four mathematical models were analyzed to identify those that best fit the profiles of *in vitro* gas production kinetics of forages commonly used in ruminant feed.

Material and Methods

This study was carried out in Dois Vizinhos, PR, Brazil, following the norms of the Committee on Animal Research and Experimentation (case no. 2014-008). The soil of the region is classified as dystroferric red nitosol, containing argillaceous texture (Bhering et al., 2008), and the area features around 5% of average slope. According to Köppen classification, the climate is a humid subtropical (Cfa).

Nine forages were evaluated: lopsided oat (*Avena strigosa* Schreb), italian ryegrass (*Lolium multiflorum* Lam.), white clover (*Trifolium repens* L.), birdsfoot trefoil (*Lotus corniculatus* L.), common vetch (*Vicia sativa* L.), African star grass (*Cynodon nlemfluensis*), Tifton-85 (*Cynodon ssp.*), Aruana guinea grass (*Panicum maximum* Jacq.), and forage sorghum hybrid (*Sorghum bicolor* × *Sorghum sudanense*). As each forage had different cut numbers and harvest years, we used only materials harvested in the second cut and from the same year, respecting the growing season of each one (Table 1). Forage harvest was performed manually, using pruning shears in an area of 0.25 m². Nitrogen fertilization in the form of urea (45% N) was shared in two applications, 50% with tillering and the remainder after the first forage cut.

For the evaluation of chemical composition (Table 2), forage samples were pre-dried in a 55 °C forced-air oven for 72 h and grounded to pass through a 1-mm sieve of a Wiley-type mill™ (Thomas Scientific). We presented the chemical composition on a dry matter (DM) basis (method 967.03; AOAC, 2019). We determined ash (ASH) by method 942.05 (AOAC, 2019). Crude fat was evaluated by method 2003.06 (Thiex et al., 2003; AOAC, 2019), using hexane (isomers mix, reagent grade) as

Table 1 - Harvest and crop management of forages used in the assays for the adjustment in the mathematical model parameters that describe the rumen degradation kinetics

Forage	Harvest year/season	Height (cm)	Nitrogen fertilization (kg·ha⁻¹·yr⁻¹)	Cut	Residue (cm)
Aruana guinea grass	2013/summer	35	120	2nd	20
African star grass	2013/summer	25	120	2nd	10
Forage sorghum hybrid	2013/summer	75	150	2nd	20
Tifton 85	2013/summer	25	120	2nd	10
Lopsided oat	2012/winter	25	120	2nd	10
Italian ryegrass	2012/winter	25	120	2nd	10
Birdsfoot trefoil	2012/winter	20	120	2nd	10
Vetch	2012/winter	30	120	2nd	20
White clover	2012/winter	20	120	2nd	10

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solvent, and crude protein (CP) was assayed indirectly by N content according to methods 984.13 and 2001.11 (Thiex et al., 2002; AOAC, 2019), in which the CP was obtained by digesting samples in a solution composed of H_2SO_4 and a mixture of Na_2SO_4 and $Cu_2SO_4.5H_2O$ in 250-mL tubes using aluminum digestion blocks, including N recovery assays with certified $NH_4H_2PO_4$. Amylase-treated neutral detergent fiber organic matter (aNDFom) was quantified through sodium sulfite and two additions of a standardized solution of heat-stable amylase, and with ash excluded (method 2002.04; Mertens, 2002; AOAC, 2019), acid detergent fiber and acid detergent lignin (ADL) were determined according to the method 973.18 (AOAC, 2019), modified by Möller (2009) after a sequential acid detergent extraction (Van Soest et al., 1991); then, readily degradable soluble sugars (CHO) were estimated by the phenol-sulfuric method (Dubois et al., 1956), in which carbohydrate concentration was estimated in aqueous solutions. The N fractions trichloroacetic acid insoluble protein, neutral detergent insoluble protein (without using sodium sulfite), and acid detergent insoluble protein were determined as described by Licitra et al. (1996).

Three replicates (bottles) per forage sample were incubated for up to 144 h. *In vitro* rumen kinetics assays were performed in a water bath at 39 °C, using 100-mL serum amber bottles sealed with butyl rubber stoppers and aluminum crimp seals. Individually, ground forage samples of approximately 0.5 g were transferred into the bottles and incubated with 40 mL reduced solution and culture medium with 10 mL of rumen inoculum, as previously described by Goering and Van Soest (1970). The culture medium, reducing solution, and inoculum were prepared as a single batch (Hall and Mertens, 2008). Rumen fluid was obtained from two three-year-old healthy cannulated Holstein steers, ±550 kg body weight. Steers were maintained in a paddock with black oat pasture and, before *in vitro* assay, supplementation was provided for eightdays, with corn silage and ground corn (1 kg/day), as recommended by Abreu et al. (2014). Briefly, the system used a gauge gas pressure, and volume was similar to the one described by Abreu et al., 2014. The pressure of the gases generated with the fermentation process was recorded by manometric readings (0-7 psi; 0.05 psi increments), and the volume was measured by using a graduated pipette (0-25 mL; 0.1 mL increments).

Gas pressure and volume rate were measured at 1, 2, 3, 6, 8, 10, 12, 16, 20, 24, 30, 36, 48, 72, 96, 120, and 144 h incubation and expressed as mL $0.1\ g^{-1}$ DM from the incubated sample. Four mathematical models of gas production kinetics were used (Zwietering et al., 1990; Schofield et al., 1994). These

Table 2 - Least squares means and confidence intervals (0.95CI) for the predicted chemical components for tropical and temperate forages used in ruminant feed

Forage	Chemical component								
	CP[1]	TCAIP[1]	NDIP[1]	ADIP[1]	ASH[1]	CF[1]	aNDFom[1]	CHO[1]	ADL[1]
Aruana guinea grass	128.6±4.72	42.4±7.78	61.0±4.93	11.1±1.15	85.1±2.79	23.4±1.11	661.2±2.05	27.9±0.71	46.5±0.88
African star grass	187.1±6.54	64.0±12.80	89.0±0.06	14.4±1.12	87.7±1.51	20.0±0.61	597.8±8.50	24.9±1.63	41.8±0.78
Forage sorghum hybrid	185.6±5.45	63.3±8.07	82.9±3.31	9.8±0.63	61.3±2.01	27.8±0.50	595.5±28.76	72.6±8.98	29.8±0.79
Tifton 85	138.2±2.63	48.4±10.86	63.5±4.75	9.2±0.56	79.0±3.53	25.2±0.53	658.5±0.96	47.0±7.97	29.4±4.01
Lopsided oat	301.2±11.40	194.4±14.45	59.8±1.17	5.4±1.27	98.0±3.41	36.0±0.56	427.3±10.93	36.9±3.75	15.6±1.41
Italian ryegrass	157.1±12.47	37.5±4.60	74.2±2.22	9.9±0.60	104.4±4.5	31.1±1.02	509.2±5.50	109.2±7.15	23.6±1.59
Birdsfoot trefoil	238.0±12.42	50.5±14.38	67.3±5.46	18.0±1.84	94.1±2.04	40.9±1.16	254.4±6.83	82.4±12.54	58.6±2.33
Vetch	222.5±7.15	48.5±16.27	80.2±14.13	17.3±0.62	93.2±0.71	36.2±0.48	321.1±4.30	40.1±2.51	49.8±2.35
White clover	254.3±0.32	60.9±3.65	94.3±4.95	14.1±0.65	113.4±3.47	43.5±0.78	291.4±11.51	125.3±8.75	28.3±3.55

CP - crude protein; TCAIP - trichloroacetic acid insoluble protein; NDIP - neutral detergent insoluble protein; ADIP - acid detergent insoluble protein; CF - crude fat; aNDFom - amylase-treated neutral detergent fiber organic matter; CHO - soluble sugars; ADL - acid detergent lignin.
[1] $g \cdot kg^{-1}$ on a dry matter basis.

models (M1, M2, M3, and M4) were fitted to the cumulative gas production profiles derived by the rumen fermentation of each forage test. For all models, V_t is the cumulative gas production over time (t; h) (Abreu et al., 2014):

M1 - Exponential: $V_t = V_f [1 – exp(–kt)] + \varepsilon$

M2 - Gompertz: $V_t = V_f\, exp\{–exp[1 + ke(\lambda – t)]\} + \varepsilon$

M3 - Schofield (M1+M2): $V_t = V_{f1} [1 – exp(–k_1 t)] + V_{f2}\, exp\{– exp[1 + k_2 e(\lambda – t)]\} + \varepsilon$

M4 - (M2+M2): $V_t = V_{f1}\, exp\{–exp[1 + k_1 e(\lambda – t)]\} + V_{f2}\, exp\{–exp[1 + k_2 e(\lambda – t)]\} + \varepsilon$

The models M1 and M2 are unicompartmental, represented by V_f as the asymptotic gas volume reached for a single pool substrate, with M1 describing first order (exponential) degradation kinetics and no lag time, while M2 is a Gompertz growth model, with discrete lag time (λ). For both, k (h^{-1}) is the fractional rate constant of cumulative gas production inferable as the digestion rate of a single pool substrate. The models M3 and M4 are bicompartmental, exhibiting one compartment of fast and another of slow degradation in the rumen, in which V_{f1} and V_{f2} describe the volume of asymptotic gas production of these two compartments, respectively. Parameter k_1 is the specific rate of gas production by degradation of the soluble fraction of rapid digestion, and k_2 is the specific rate of gas production for degradation of potentially degradable insoluble fraction of slow digestion (h^{-1}). In M3, the fast digesting pool is fermented as a first-order process without lag, and the second pool follows a logistic pattern with a lag time (λ; h^{-1}). Model M4 was designed to fit sigmoid-shaped patterns in which fast and slow digesting pools yield asymptotic gas volumes (V_{f1} and V_{f2}) at k_1 and k_2 rates (h^{-1}) after a common lag time (λ; h^{-1}) for both pools (Abreu et al., 2014). The term e is the base of natural logarithms and ε the random error, for all models.

Four additional parameters were estimated from the different nonlinear models (M1 to M4) and considered by the Marquardt algorithm from the nonlinear procedure of SAS (Statistical Analysis System, version 9.4). The likelihood of M1 to M4 to reproduce the profile of gas production was determined by the calculation of the corrected Akaike criterion ($AICc_r$) (Sugiura, 1978). The $AICc_r$ was calculated from the residual sum of squares (RSS), the number of parameters estimated for the model, including random error (Θ_r). From the $AICc_r$, some derived functions were calculated as the difference between each $AICc_r$ value and the minimum $AICc_r$ among models (Δ_r), likelihood probability (w_r), and relative likelihood (ER_r) (Burnham and Anderson, 2004; Vieira et al., 2012).

For the model to be considered for reproducing the observed data behavior and reduce the loss of information, the value of Δ_r had to be between 0 and 2. Values of Δ_r higher than 2 and smaller than or equal to 10 indicate their performance is acceptable, and values higher than 10 suggest that the model fails to reproduce the data and minimize the loss of information (Burnham and Anderson, 2004; Vieira et al., 2012).

A value of $ER_r = 1$ is used for selecting the best model. Models with values of ER_r higher than 1 and smaller than or equal to 20 will be considered less likely models, and those with ER_r higher than 20 will be the worst choices (Vieira et al., 2012). With regard to W_r, values higher than 0.8 were considered credible representations of reality, between 0.5 and 0.8 less likely, and below 0.5 were not considered reliable representations of the observed degradation profile (Burnham and Anderson, 2004; Vieira et al., 2012).

Results

The model M3 was considered the best choice for Aruana guinea grass, African star grass, forage sorghum hybrid, Tifton 85, and birdsfoot trefoil; M1 was the best choice for lopsided oat 'IPR 61', Italian ryegrass, vetch, and white clover (Table 3); M4 was considered a second choice for African star grass and Tifton 85; and M2 was the worst option for almost all forages, except for Italian ryegrass, in which M4 was the worst choice (data not shown).

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Table 3 - Information criterion of the two best mathematical models to describe *in vitro* gas production kinetics for tropical and temperate forages used in ruminant feed

Forage	Model	Akaike information criterion and the derived measures				
		$AICc_r$	Δ_r	W_r	ER_r	Θ_r
Aruana guinea grass	M3	−55.66	0	1	1	6
	M1	−37.55	18.12	0	8600.59	3
African star grass	M3	−1.16	0	0.98	1	6
	M4	7.93	9.09	0.01	94.16	6
Forage sorghum hybrid	M3	−101.8	0	0.994	1	6
	M1	−91.63	10.17	0.006	161.53	3
Tifton 85	M3	−22.04	0	0.998	1	6
	M4	−9.48	12.56	0.002	532.68	6
Lopsided oat	M1	10.53	0	0.603	1	3
	M3	11.73	1.2	0.33	1.82	6
Italian ryegrass	M1	46.97	0	0.904	1	3
	M3	51.47	4.5	0.096	9.46	6
Birdsfoot trefoil	M3	−48.79	0	1	1	6
	M1	−29.07	19.72	0	19156.67	3
Vetch	M1	−33.3	0	0.688	1	3
	M3	−31.71	1.58	0.312	2.21	6
White clover	M1	−62.65	0	1	1	3
	M3	−34.19	28.46	0	1512870.98	6

$AICc_r$ - corrected Akaike information criterion; Δ_r - difference between each $AICc_r$ value and the minimum $AICc_r$ among models; W_r - model probabilities; ER_r - evidence ratios; Θ_r - number of parameters estimated for the model including random error.

In all situations that M3 was the model with best fit, W_r was higher than 0.8, indicating that this model could be considered a likely representation of degradation. However, when M1 fitted better for lopsided oat 'IPR 61' and vetch, W_r values ranged from 0.5 to 0.8, meaning the model would be considered a less likely representation of observations. For Italian ryegrass, the W_r value of M1 was higher than 0.8. The second-choice models always showed W_r values smaller than 0.5, i.e., to estimate the degradation profiles, these models should not be considered likely representations.

The estimated values in V_{f1} were higher than V_{f2} as k_1 values were higher than k_2 for all the kinetic profiles in which M3 was the best choice. The only exception was Tifton 85 profile, whose V_{f2} value was higher than the V_{f1} value. Sorghum hybrid was the only forage with an estimated lag time (λ) equal to zero. The other λ estimates varied from 1.2 h for birdsfoot trefoil to 7.3 h for African star grass. The estimates of the maximum gas production (V_{f1} and V_{f2} for M3 and V_f for M1) varied from 24 mL 0.1 g^{-1} DM for vetch to 31 mL 0.1 g^{-1} DM for Tifton 85.

Discussion

The exponential model (M1) fitted well to the gas production profile of almost all temperate forages (lopsided oat 'IPR 61', Italian ryegrass, vetch, and white clover), whose fiber content is lower (Table 2), and digestibility is commonly higher than those of tropical forages (Van Soest, 1994). This model describes the rumen digestion process as first-order kinetics without lag time. Still, the single pool model that represents the fractional rate of gas production is directly proportional to the substrate availability, i.e., it is independent of the microbial mass (Schofield et al., 1994). It was not possible to identify two distinct groups in the degradation profile of temperate forages, because the neutral detergent soluble and insoluble fractions would not be so distinct in relation to rumen degradation.

The unicompartmental model M1 did not fit the gas production profile of birdsfoot trefoil (Tables 3 and 4). Despite being a temperate forage, birdsfoot trefoil had the highest concentration of ADL in this study (Table 2). Leguminous forages present higher lignin content (due to a phenolic

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compound bound to the insoluble fraction of the fiber) when compared with grasses (Van Soest, 1994; Gomes et al., 2011; Spínola et al., 2017). The digestibility of the fiber fraction in the rumen was hampered by the high concentration of ADL; therefore, lignin content limits cell wall digestibility (Cherney and Mertens, 1998; Raffrenato et al., 2017). As observed by Fluck et al. (2013), the increase in ADL content causes reduction in bacterial adhesion, total *in vitro* gas production, and *in vitro* gas production rate of tropical legumes. The impact of lignin on plant degradability is even greater than the effects of tannin or any other chemical component (Fluck et al., 2013). Although tannins have not been evaluated in this study, they can cause negative effects, mainly on the palatability of the food and complexation with proteins in the rumen (Naumann et al., 2017); however, it can be beneficial for animal performance, in some situations (Waghorn, 2008).

The ADL:aNDFom ratio for the birdsfoot trefoil is 0.23; for vetch the value is 0.16, and for white clover it is 0.10. It demonstrates the high proportion of ADL in birdsfoot trefoil compared with the other legumes used in this study. The ADL:aNDFom ratio of the grasses ranged from 0.04 for Tifton 85 and lopsided oat 'IPR 61' to 0.07 for the Aruana guinea grass and African star grass; these are lower values than the ones found for legumes.

The model M2 describes a single pool gas production profile with a discrete lag time (Schofield et al., 1994) that was sometimes observed in degradation profiles. This was found by Malafaia et al. (1998) in data from gas production kinetics of several tropical grasses. However, none of the profiles evaluated in the present study had an evident lag time (Table 4), and, consequently, M2 was not the choice for any of the forages. Only for the profiles in which M3 was the best choice, there was an estimated value for lag time. This lag time is associated with the degradation of the FC.

The good quality of M3 fit to the gas production profile of Tifton 85, African star grass, Aruana guinea grass, and forage sorghum hybrid was expected due to the higher fiber content (Table 2), because, compared with temperate forages, both may show lower digestibility, which is characteristic of tropical grasses (Van Soest, 1994; Mahyuddin and Purwantari, 2009; Eustáquio Filho et al., 2010). The nutritional characteristics of the tropical grasses describe a degradation profile with two distinct pools of degradation: one fast (for the soluble fraction) and one slower (for FC).

Among temperate legumes, the lag time of M3 was also the best choice for birdsfoot trefoil (Tables 3 and 4). This forage has the highest ADL concentration among the plants used in this study (Table 2). The lignin content limits the maximum potential of cell wall degradation (Van Soest, 1994; Carvalho and Pires, 2008; Ogeda and Petri, 2010), and this could reduce the degradation rate of birdsfoot trefoil fiber fraction.

Table 4 - Least squares means of the estimate parameters and confidence intervals (0.95CI) of the mathematical models of *in vitro* gas production kinetics chosen for tropical and temperate forages used in ruminant feed

Forage	Model	V_f	κ	V_{f1}	k_1	V_{f2}	k_2	λ
Aruana guinea grass	M3	-	-	19.7±5.62	0.048±0.0178	10.3±4.94	0.011±0.0044	6.8±10.90
African star grass	M3	-	-	13.1±5.29	0.079±0.0413	12.6±4.96	0.014±0.0054	7.3±12.40
Forage sorghum hybrid	M3	-	-	22.2±3.56	0.036±0.0574	5.7±3.66	0.033±0.0026	0
Tifton 85	M3	-	-	8.4±1.77	0.136±0.0285	22.7±1.82	0.018±0.0013	9.6±6.93
Lopsided oat	M1	25.0±0.60	0.054±0.0037	-	-	-	-	-
Italian ryegrass	M1	27.8±0.85	0.053±0.0046	-	-	-	-	-
Birdsfoot trefoil	M3	-	-	23.6±1.91	0.068±0.0090	4.7±2.56	0.006±0.0079	1.2±28.09
Vetch	M1	24.2±0.19	0.058±0.0014	-	-	-	-	-
White clover	M1	26.8±0.29	0.064±0.0020	-	-	-	-	-

V_{f1} and V_{f2} are the maximum volumes of gas produced by degradation of the fast and slow digestion fractions, respectively (mL 0.1 g^{-1} DM); V_f is the asymptotic gas volume reached for a single pool substrate; k_1, k_2, and κ are the specific rates of gas production of the fast and slow digestion fractions and of a single substrate, respectively (h^{-1}); λ = lag time (h^{-1}).

Temperate forages reached maximum gas production between 48 and 72 h (Figure 1), while for tropical forages, the same occurred only after 72 h. The faster degradation rates of the temperate grasses were due to the lower fiber content (Table 2) and plant anatomy, especially of the leaf. Temperate forages have lower sclerenchyma content in the leaves than tropical forages; sclerenchyma and xylem are highly lignified tissues that limit rumen degradation (Akin, 1989).
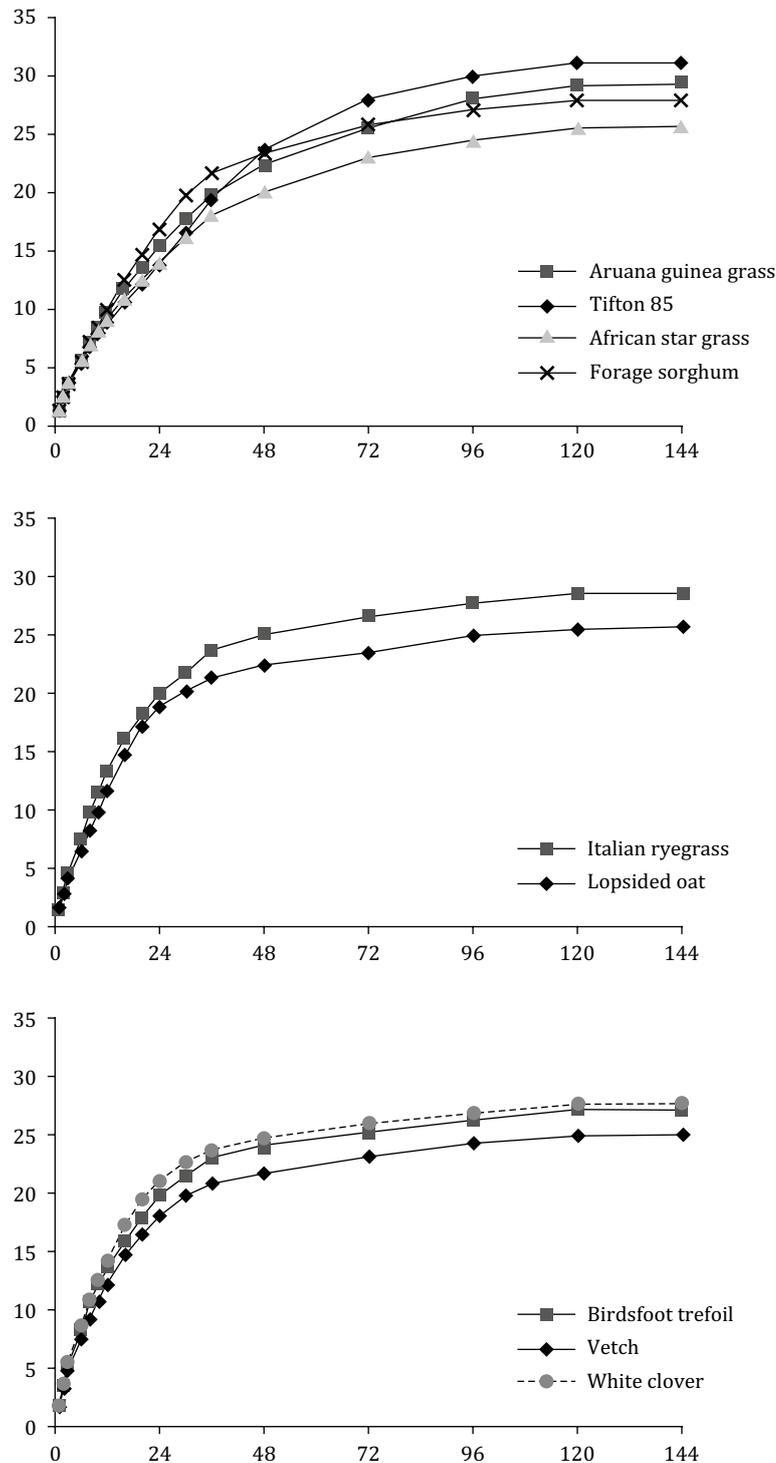
X-axis = incubation time (h); Y-axis = volume of gas (mL 0.1 g^{-1} DM).
Continuous lines represent the values fitted by the model chosen for each forage.

Figure 1 - Profiles adjusted to observed data.

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Tifton 85 was the only forage with an estimated value of V_{f1} lower than that of V_{f2} (Table 4). The hypothesis is that the low lignin content of Tifton 85, when compared with other tropical grasses (Table 2), facilitated degradation of the fibrous fraction. Although the lignin content of Tifton 85 was close to that obtained for sorghum, the aNDFom content in this forage was lower, and, therefore, the disparity between V_{f2} and V_{f1} values was not as large as in Tifton 85. In addition, Tifton 85 has low CHO:aNDFom ratio (approximately 0.11), thereby justifying the low production of gases resulting from the degradation of CHO.

Conclusions

The bicompartmental model, without lag time in the first compartment, fits better for tropical forages with high fiber content and low levels of nonfibrous carbohydrates and protein.

The exponential model without lag time has a better quality of fit for forage *in vitro* gas production profiles with high quantity nonfibrous carbohydrates and low lignin contents.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: D.S. Henrique. Formal analysis: D.S. Henrique. Investigation: J.G. Oliveira and D.S. Henrique. Methodology: J.G. Oliveira, D.S. Henrique, M.L.C. Abreu and Atoji-Henrique, K. Project administration: J.G. Oliveira and L.R.R. Mayer. Writing-original draft: J.G. Oliveira and D.S. Henrique. Writing-review & editing: J.G. Oliveira, D.S. Henrique, A.C. Fluck, O.A.D. Costa and Atoji-Henrique, K.

Acknowledgments

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