Use of the gamma function in equations which describe ruminal fermentation and -outflow rates for the prediction of voluntary intake and protein degradation

J.P. Pienaar* and C.Z. Roux
Animal and Dairy Science Research Institute, Private Bag X2, Irene 1675, Republic of South Africa

Received 15 May 1988; accepted 17 October 1988

Five models were studied for goodness of fit to *in sacco* organic matter disappearance. Except for the first-order model, all the other models showed an accurate and unbiased fit, although in some cases this was achieved by unrealistic parameter estimates or an increase in the number of parameters that need to be estimated. The first-order model showed a biased fit as indicated by a slope which is significantly larger than 1 for the regression between observed and predicted values. Marker passage at the ileum was satisfactorily described by the gamma retention time distribution in 90% of the cases. Only the curve of one sheep, which had a very irregular flow pattern, could not be fitted accurately by this function. The integer form of the gamma distribution of retention time may be used to combine outflow and fermentation in one equation. This equation describes the disappearance of fermentable OM, when calculating intake.

Die akkuraatheid waarmee vyf modelle *in sacco* organiese-materiaal(OM)-verdwyning beskryf, is bepaal. Behalwe vir die eerste-ordemodel, het al die modelle 'n akkurate en onsydige passing gelewer, hoewel dit in sekere gevalle verkry is deur onrealistiese beramings van parameters, of deur 'n vermeerdering van die aantal parameters wat gepas moet word. Die eerste-ordemodel het 'n sydige passing gelewer soos aangetoon deur die helling tussen die waargenome en voorspelde waardes wat betekenisvol groter as 1 was. Die vloei van merker by die ileum is bevredigend beskryf deur die gamma-retensietydmetode. Slegs een skaap se kurwe van merker-uitskeiding was baie veranderlik en kon nie akkuraat deur die funksie gepas word nie. Die heeltalvorm van die gamma-verdeling van retensietyd kan gebruik word om uitvloei en fermentasie in een vergelyking te kombineer. Hierdie vergelyking beskryf die verdwyning van fermenteerbare OM wanneer inname bereken word.

Keywords: Fermentation, intake prediction, models, passage, rumen.

* Author to whom correspondence should be addressed.

Introduction

It is a well-established fact that voluntary feed intake is a function of rumen fill, as well as removal rates from the rumen, in the case where intake is limited by rumen fill (Roux & Meissner, 1984).

Both fermentation and outflow from the rumen have been estimated by indirect methods such as the *in sacco* technique (Ørskov & McDonald, 1979), the *in vitro* approach (Mertens & Loften, 1980), and the use of markers (Graham & Williams, 1962). In order to estimate voluntary feed intake from these measurements, fermentation and outflow have to be combined in a single equation, together with other variables, which would then allow the situation in the rumen to be described at steady-state intake. This was done by Pienaar, Roux, Morgan & Grattarola (1980) for first-order equations. However, both outflow and fermentation show significant deviations from first-order kinetics (Mertens & Loften, 1980; McDonald, 1981; Pond, Matis & Ellis, 1982; Mahlooji, Ellis, Matis & Pond, 1984; Pienaar & Roux, 1984), which consist of a phase of increasing activity at the onset of both the outflow and fermentation processes.

Mertens & Loften (1980) and McDonald (1981) accommodated this deviation from first-order kinetics in their models by including a lag (dead) phase at the onset of fermentation. This correction implies that a phase of no activity immediately precedes a phase of maximum activity, at which a first-order kinetics set in at a specific point in time. It is difficult to imagine such a situation in the rumen.

The gamma function (Law & Kelton, 1982) appears to eliminate the problems of the model of McDonald (1981), since it does not include a lag (dead) phase. Rather, it can accommodate a phase in which activity increases from virtually zero to maximum. This model makes use of two parameters, one describing shape (α) and one the scale (β) of the curve. These two parameters give this model more flexibility than a simple first-order model. Furthermore, some functional significance may also be ascribed to these two parameters. The inverse of parameter β is similar to a first-order rate constant, whereas parameter α modifies the shape of the first-order curve. When $\alpha = 0$, the equation reduces to that of a first-order curve. As α increases, the effect of a delay (slow starting) phase is superimposed on the parameter β and disappearance rate is not only slowed down, especially at the onset, but is also smoothly carried over into the later stages of fermentation. This description of events would seem to be more appropriate than a lag phase, which is inappropriate to rumen digestion kinetics.

The effect of α on the mean of the gamma distribution ($\alpha * \beta$) may also be obtained by simply subtracting β from the mean;

$$(\alpha * \beta) - \beta \; . \qquad (1)$$

For example, if the mean of the gamma distribution ($\alpha * \beta$) = 48 h and β = 30 h, the effect of (α = 1,6) on the total curve is 48 − 30 = 18 h.

Attempts to relate fermentation rate or digestibility to voluntary intake are not uncommon (Gill, Conrad & Hibbs, 1969; Hovell, Ng'ambi, Barber & Kyle, 1986).

However, since the relationships between these factors and intake are not linear, and are influenced by many other factors (Pienaar *et al.*, 1980), it would seem logical to incorporate these relevant factors into a single equation which describes intake in terms of rumen digestion kinetics. By doing so, the numerical relationship of these factors to voluntary intake may be established under field conditions. This has been done for cases where outflow and fermentation were described in terms of first-order equations (Pienaar *et al.*, 1980). However, since neither outflow nor fermentation was adequately described by first-order equations, the data were re-examined in terms of the intake equation derived in this paper.

In this study, the gamma function is fitted to both *in sacco* OM disappearance (fermentation) and faecal marker excretion (passage), and the goodness of fit is demonstrated. Other functions, often used to describe fermentation, are compared to the gamma function in terms of accuracy of fit. General equations for intake and protein degradation are also constructed from equations where outflow and fermentation are described in terms of gamma probability distributions.

Materials and Methods

Animals and diets

Fermentation study

The animals used in the fermentation studies were six mature, rumen-cannulated sheep fed two roughage diets. These diets consisted of either ground lucerne hay or ground maize-cob leaves, supplemented with micro and macro minerals, some molasses, urea and fish-meal, so as to exceed the minimum mineral and protein requirements for maintenance (NRC, 1975). The animals were accustomed to being housed individually in metabolism crates and to automatic feeders set to deliver six aliquots of feed, one every 4 h.

Marker passage study

The animals used in the marker passage study were 12 mature sheep, fitted with rumen and simple ileal cannulae. Although the same diets were used as in the fermentation studies, these were fed either in a chopped or finely ground form (Pienaar & Roux, 1984).

Experimental procedures

In sacco *technique*

The method described by Cronjé (1983), using defined aperture polyester material with a pore size of 53 μm, was used. Bags were removed after 3, 6, 9, 12, 24, 48 and 72 h of incubation. Samples of each diet that was fed during the fermentation studies were incubated simultaneously in three sheep and were repeated over two periods (Mehrez & Ørskov, 1977).

Procedure for marking solid particles

The protocol previously described by Pienaar & Roux (1984), was used. Samples of each diet were labelled with the (^{51}Cr)-mordant, and were mixed into the rumen digesta of each sheep. Spot samples were collected through the ileal cannulae at short intervals.

Calculations

Calculation of fermentation parameters

Fermentation rate was described by each of five models. The first two models may be seen as first-order; one describing fermentation up to 24 h and the other, up to 48 h:

$$y = a e^{-kt} \quad (2)$$

where y represents the mass of fermentable OM in the bag, a the mass at onset of fermentation, k the first-order rate constant and t denotes time.

The third model (equation 3; McDonald, 1981), also based on a first-order approach with rate constant c and a fraction b' that will ferment in time, includes a rapidly soluble fraction a or a' as well as a lag time, t_0. The percentage (p) fermented at time t is represented by:

$$p_1 = a \text{ for } t \leqslant t_0$$
$$p_2 = a' + b' (1 - e^{-ct}), \text{ for } t > t_0. \quad (3)$$

The fourth, or heterogeneous rate constant model (Mahlooji *et al.*, 1984), may be described as a moment-generating function of a gamma distribution with α and β as spread parameters, and where D denotes the digestible fraction, τ the time delay, and t the time:

$$F(t) = D \text{ for } 0 \leqslant t < \tau \text{ and}$$
$$F(t) = D [1 + \beta (t - \tau)]^{-\alpha} \text{ for } t \geqslant \tau. \quad (4)$$

The fifth model we propose to call the gamma retention time model. In contrast to previous descriptions, we postulate that the disappearance of potentially fermentable OM may be described by a gamma probability distribution (equation 5). In statistical terms, the retention time of potentially fermentable OM follows a gamma distribution. This method was preferred to the method of Mertens & Loften (1980) as well as to that of McDonald (1981), since it includes a time of increasing activity (called a delay phase), instead of the lag (dead) phase used by the others. In mathematical terms, the model may be stated as:

$$\Delta y \propto t^{\alpha - 1} e^{-t/\beta}, \quad (5)$$

where Δy = mass of OM fermented in an infinitesimal interval of time at time = t.

The method used to calculate the two parameters of the gamma distribution, *viz.* α (shape parameter) and β (scale parameter), is based on calculating mean retention time (MRT, Graham & Williams, 1962) as well as mean retention in log time, ln(t), by using Table 5.11 of Law & Kelton (1982).

Goodness of fit of all the functions used to describe fermentation was tested by comparing predicted values calculated from estimates of the parameters of the function studied, with actual values observed in the nylon bags. For example, the cumulative distribution of the gamma function was calculated from estimates of the two parameters, α and β, and was compared to the actual values (mass of fermentable OM in bag).

Goodness of fit was assessed from an evaluation of the slope (a) and intercept (b) parameters obtained from a linear regression of predicted values against actual observations, where values of a = 1 and b = 0, together with high coefficient of association (r^2) values, suggest that the model may indeed accurately reflect reality. This approach also allows a number of graphs to be combined, thereby increasing the statistical accuracy of the determination.

Calculation of marker passage parameters

Goodness of fit of the gamma mean retention time model to marker passage at the ileum was also studied. It was postulated that the time of appearance of labelled particles at the ileum (or abomasum) follows a gamma probability distribution. Similar to the fermentation model, the cumulative distribution of the gamma function was calculated from the two parameters, α and β. These derived data were compared to actual values of marker passage obtained at the ileum. The method used to calculate marker passage at the ileum has been described by Pienaar & Roux (1984), and is known as the ileal appearance method. In short, it comprises the calculation of marker passage from a single injection of marker into the rumen, where spot samples of digesta were taken at fixed time intervals, rather than total collection of digesta. This method has been previously validated for use under steady-state conditions (Pienaar & Roux, 1984). The method preferred to calculate the two parameters, α and β, of the gamma distribution is based on calculating MRT (Graham & Williams, 1962) as well as mean retention in log time ln(t), by using Table 5.11 of Law & Kelton (1982). MRT is calculated according to the following formula:

$$\bar{t} = \Sigma \tfrac{1}{2}C(t' - t)(t' + t) / \Sigma \tfrac{1}{2}C(t' - t) \qquad (6)$$

where C = number of counts in the sample for the interval t' to t. For mean retention in log time, the expression '$\ln[(t' + t)/2)$' was substituted for $(t' + t)/2$ in the same equation.

The intake equation

Feed intake was described by Roux & Meissner (1984) as the mass of feed in the rumen divided by the MRT of feed in the rumen. Equation 7 may be used to describe this relationship:

$$df/dt = Z / \sum_{i=1}^{n} p_i t_i, \qquad (7)$$

where df/dt = feed intake, Z = total amount of feed in the rumen, p_i = the proportion of component i in the feed, t_i = the mean retention time of component i, and n = total number of components. This approach is only valid under steady-state conditions or when such conditions are approximated by averaging parameters over suitable time periods (Pienaar, Roux & Cronjé, 1989).

For the purpose of this study feed was divided into three fractions. The first fraction was defined as the immediately soluble, digestible fraction with a MRT = 0 h. This fraction will not have a measurable effect on rumen fill. The second fraction is the insoluble, potentially digestible fraction which disappears as a result of both fermentation and outflow from the rumen, with each process following gamma mean retention kinetics as described above. The third fraction is the potentially indigestible fraction which disappears by outflow only, and also follows gamma retention time kinetics. In a previous paper, Pienaar, Roux & Cronjé (1989) have shown that this may be a reasonable assumption, and showed good agreement between *in sacco* OM disappearance and *in vivo* OM disappearance, both described in terms of MRT.

In vivo OM disappearance includes disappearance by both fermentation and outflow, both acting independently on the same pool of potentially fermentable OM. Therefore, when *in sacco* or *in vitro* estimates of OM disappearance have to be used to estimate *in vivo* disappearance (retention time), the two gamma functions may be combined under the assumption that they act independently on the same pool. The general form of mean retention times for two integer gamma functions acting independently on the same pool, is given in Appendix 1, equation 15. Since the general equation is not very convenient to work with, it has been solved for a few situations of α_0 and α_1 which are commonly encountered in practice. These are presented in equations 8–11.

The situation where $\alpha_0 = 1$ and $\alpha_1 = 1$ is equivalent to two first-order equations working on one pool. MRT is given by:

$$\bar{t} = (1/\beta_0 + 1/\beta_1)^{-1}. \qquad (8)$$

where α_0 and α_1 represent shape parameters and β_0 and β_1 scale parameters of the gamma functions which describe outflow and fermentation of fermentable OM, respectively.

For the situation $\alpha_0 = 2$, $\alpha_1 = 2$, MRT may be described by

$$\bar{t} = 2(1/\beta_0 + 1/\beta_1)^{-1} + (2/\beta_0\beta_1)(1/\beta_0 + 1/\beta_1)^{-3}. \qquad (9)$$

For the situation $\alpha_0 = 2$, $\alpha_1 = 1$, MRT may be described by

$$\bar{t} = (1/\beta_0 + 1/\beta_1)^{-1} + (1/\beta_0)(1/\beta_0 + 1/\beta_1)^{-2}, \qquad (10)$$

and for $\alpha_0 = 1$, $\alpha_1 = 2$, MRT may be described by

$$\bar{t} = (1/\beta_0 + 1/\beta_1)^{-1} + (1/\beta_1)(1/\beta_0 + 1/\beta_1)^{-2}. \qquad (11)$$

It is interesting to compare these forms of the gamma function with that of a single gamma distribution which has a MRT of $\alpha\beta$. The single gamma distribution (MRT = $\alpha\beta$) is the appropriate form to describe the outflow of non-fermentable OM, since only one gamma acts on one pool.

The method described above to fit the gamma function is suitable for fitting the general form of the gamma function and may yield non-integer values for α. Since the equations could only be obtained in explicit mathematical form for integer gammas it is suggested that, for the purpose of calculating MRTs, α be rounded to both the integer values larger and smaller than the observed value.

The relevant β values may then be calculated from the mean values as $\beta = \bar{t}/\alpha$, where α is expressed in integer form. MRT values may then be calculated for both sets of integer values of α. An estimate of MRT may then be obtained by interpolation. It is suggested that, until such time as improved estimates are obtained, those found by Pienaar *et al.* (1980) should be used for the outflow of fermentable OM on chopped roughage diets. The MRT value of 81,7 h obtained, was assumed to be a first-order estimate, thus being associated with a value of $\alpha_0 = 1$.

The application of these processes to obtain voluntary feed intake or protein degradability is given in Appendix 2.

Results

Fermentation

The goodness of fit of the different models to *in sacco* fermentation is shown in Figures 1 to 4 and is summarized in Table 1. The simple first-order model (Model 1) shows values for fermentable OM in the bag up to 48 h. The observed mass of fermentable OM plotted against the mass predicted by the first-order equation is presented in Figure 1.

Figure 1 shows the comparison based on 80 data points. The mean of the observed values (Table 1) was 1004 mg, compared to the mean of the predicted values of 897 mg. Although the intercept of −40,37 ± 46,86 did not differ significantly from 0, the slope of the regression (1,163 ± 0,040) differed significantly from 1 ($P \leq 0,01$). This suggests that first-order kinetics may not describe *in sacco* fermentation adequately.

The model described by McDonald (1981) – Model 2, was used to obtain observed versus predicted values for percentage degradation *in sacco*. These results are presented in Figure 2. This model correlated well with observed values, in that the intercept of −0,672 ± 0,694 was non-significant, the slope of 1,010 ± 0,013 did not differ significantly from 1, and the coefficient of association (r^2) was found to be 0,987. The mean of the predicted percentage degradation was 49,3%, compared to the mean of the observed degradation of 49,2%. It seems that the onset of fermentation, shown at the lower percentage degradability in Figure 2, is associated with a larger variation around the straight line. However, the fit remains good, resulting in an accurate and unbiased mean prediction.

The model of Mahlooji *et al.* (1984) – Model 3 – was also used to predict the mass of fermentable OM in the bag. Once again, calculated values were compared to the observed mass of fermentable OM in the bag. The results are presented in Figure 3, which also shows an accurate (close) and unbiased fit to a straight line, with a non-significant intercept of 3,48 ± 16,31 and a slope of 0,943 ± 0,012 (not significantly different from 1). The coefficient of association (r^2) of the regression was found to be 0,989.

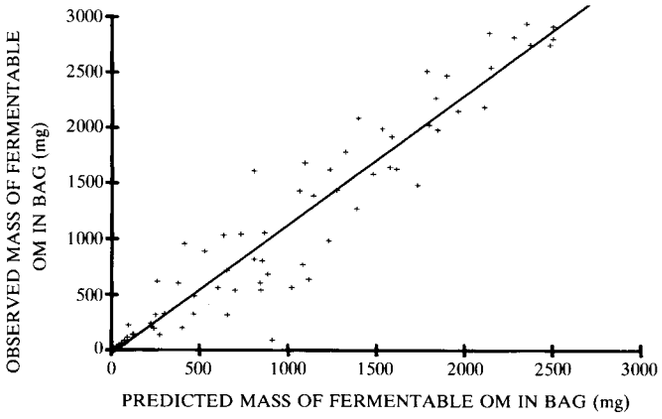

Figure 1 Goodness of fit of the first-order model to OM disappearance *in sacco* is shown by comparing the observed mass of fermentable OM *in sacco* with the mass of fermentable OM *in sacco* predicted by the model.

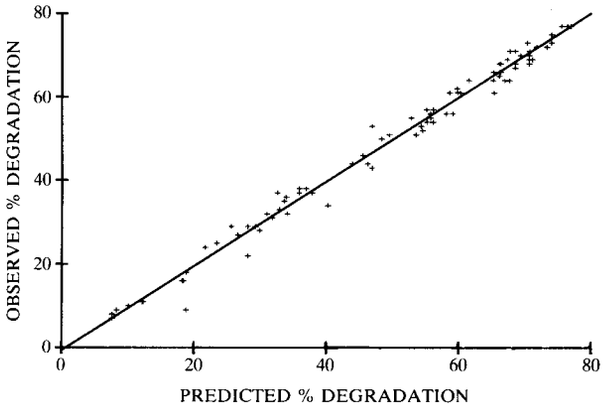

Figure 2 Goodness of fit of the model by McDonald to OM disappearance *in sacco* is shown by comparing the observed mass of fermentable OM *in sacco* with the mass of fermentable OM *in sacco* predicted by the model.

Table 1 Accuracy of fit of four models to *in sacco* fermentation and marker rate of passage

	Intercept		Slope		Goodness of fit		
Model	Mean (± *SE*)	Significance from 0	Mean (± *SE*)	Significance from 1	Predicted mean	Observed mean	Coefficient of association (r^2)
Model 1	–40,4 ± 46,9	NS[a]	1,164 ± 0,040	$P \leq 0,0001$	897,6	1004,1	0,917
Model 2	− 0,67 ± 0,69	NS	1,01 ± 0,013	NS	49,3	49,2	0,987
Model 3	3,48 ± 16,31	NS	0,943 ± 0,012	NS	1034	1043	0,989
Model 4	21,3 ± 24,5	NS	0,987 ± 0,014	NS	1087	1043	0,978
Marker passage	− 4,3 ± 6,6	NS	0,998 ± 0,22	NS	195,7	191,2	0,910

[a] Not significant.

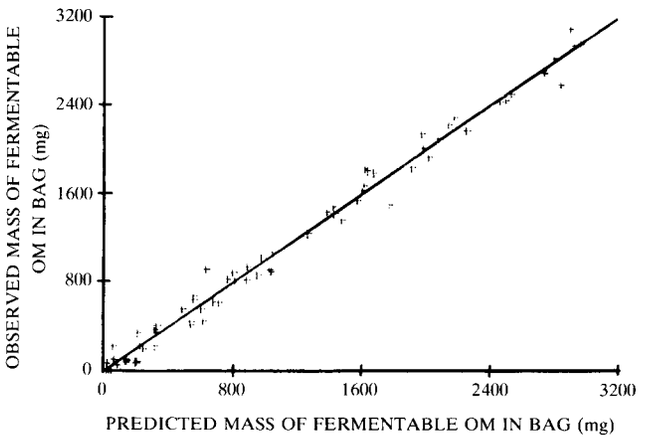

Figure 3 Goodness of fit of the model by Mahlooji *et al.* (1984) to OM disappearance *in sacco* is shown by comparing the observed mass of fermentable OM *in sacco* with the mass of fermentable OM *in sacco* predicted by the model.

The mean of the predicted values (1034 mg) was found to be very close to that of the observed values (1043 mg).

The goodness of fit of the gamma retention time model (Model 4) to fermentation *in sacco* is shown in Figure 4, which is a summary of 12 individual curves, giving a total of 75 data points. The linear regression resulted in an intercept of $-21,3 \pm 24,5$ (non-significantly different from 0) and a slope of $0,980 \pm 0,017$ (non-significantly different from 1). Besides comparing all of the predicted values to all observed values, the slopes and intercepts were calculated for individual sheep and the means of slopes and intercepts obtained. These mean values showed the same pattern that was obtained with a common line, and a non-significant mean intercept of $31,15 \pm 16,42$ and a mean slope of $0,987 \pm 0,014$ were found. Tests based on fitting a line common to all the data depend on assumptions that differ from those obtained on the average parameters from individual lines for their validity. Hence their agreement is reassuring.

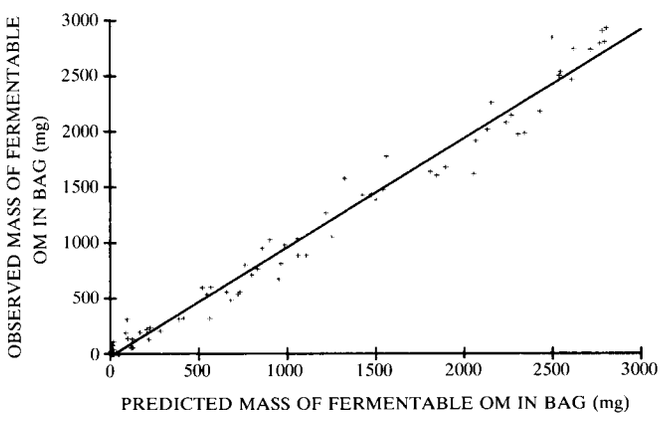

Figure 4 Goodness of fit of the gamma distribution to OM disappearance *in sacco* is shown by comparing the observed mass of fermentable OM *in sacco* with the mass of fermentable OM *in sacco* predicted by the model.

All values may therefore be plotted together, resulting in a regression with a coefficient of association (r^2) of 0,987 and a mean of the observed values of 1043 mg, as compared to the mean of 1087 mg for the predicted values. From this, it appears that the gamma mean retention time method may also give an unbiased and accurate fit of *in sacco* fermentation. It should be borne in mind that this method fits only two parameters to the data set, whereas some of the previous techniques fitted four parameters.

Marker passage

Figure 5 shows observed counts in ileal digesta versus counts calculated from the cumulative distribution of the gamma function. Linear regression of the calculated results of nine sheep on two diets against observed values resulted in a non-significant intercept of $-4,2 \pm 6,6$ (Table 1) and a slope of $0,998 \pm 0,022$ (non-significantly different to 1). The total regression contains 215 data points and the mean of the predicted counts is 195,7, whereas that of the observed counts is 191,2. The values obtained when data from individual sheep were used resulted in non-significant intercepts and slopes not different to 1, except for one sheep with a very irregular flow pattern which the gamma distribution could not accommodate. Nevertheless, when the values for that sheep were also included in the regression, a coefficient of association (r^2) of 0,91 was obtained. When the values of the sheep with the irregular flow pattern were excluded, the slope and intercept were not significantly altered, while the coefficient of association (r^2) improved.

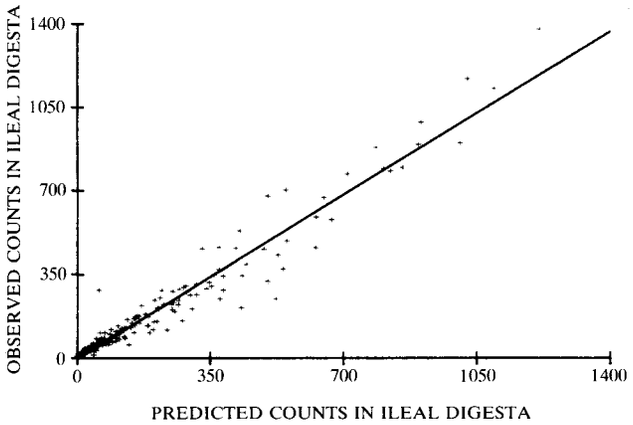

Figure 5 Goodness of fit of the gamma distribution to marker passage in ileal digesta is shown by comparing the observed counts in ileal digesta to the counts predicted by the model.

Instead of merely comparing all the predicted counts to all observed counts, the slopes and intercepts were also calculated for individual sheep and the means of slopes and intercepts were obtained. The mean slope ($1,042 \pm 0,040$) and intercept ($-8,59 \pm 7,46$) obtained in this manner, were not significantly different from 1 and 0 respectively. Tests based on fitting a common line or on obtaining mean parameters from individual lines, depend

on different assumptions for their validity, thereby supporting the argument that their agreement is significant.

Discussion

The closeness of fit of the gamma function with both fermentation and outflow (Figures 4 & 5) shows that this function has enough flexibility to describe both outflow and fermentation kinetics with sufficient accuracy. The slight bias observed in the 10 points above 2500 mg (Figure 4), indicates the possible existence of a lag (dead) phase in addition to the delay phase associated with the gamma distribution. Including such a lag phase will seriously complicate matters in the case of the gamma distribution. A lag time plus two additional parameters will have to be estimated by iterative least squares methods as was done by Mahlooji *et al.* (1984). The effect of the lag phase does not appear to be serious enough to cause concern at present. This conclusion is made from the slopes and intercepts shown in Figure 4 and Table 1.

Since MRT is calculated directly, the existence of a lag phase will have no effect on the accuracy of estimation of MRT. From the method used to estimate α and β (Law & Kelton, 1982), it may be concluded that an ignored lag phase may be the cause of bias in the separation of MRT into the shape and scale parameters and consequently on the calculations in which they are used individually. However, the model fits the data with at least the same accuracy as the generally accepted model of McDonald (1981) and also with an accuracy that is comparable to that of the model of Mahlooji *et al.* (1984). This indicates that the bias in the separation between α and β is probably very small and in any case will have a very small effect on the calculation of a combined MRT (the calculation in which they are used individually). It may be emphasized that this accuracy of the retention time model is obtained from the fit of only two parameters. This is in contrast to the four parameters used by other models. The gamma function in the integer form (Erlanger gamma) has some very convenient mathematical properties which allow it to be combined in a single equation which describes intake. The first-order model has the same mathematical properties and was used as such by Pienaar *et al.* (1980). However, the present results as well as other work (see Introduction), have shown that it lacks flexibility to describe outflow and fermentation accurately.

All the other more complex and also more flexible functions such as the ones mentioned above as well as the 'Weibull' (Law & Kelton, 1982) can, however, not be combined to give intake in an explicit mathematical form. The answers will have to be obtained by numerical integration unless it can be specified that the values for t_0 are similar for both the outflow and fermentation of fermentable OM. This is also true for the models of Mahlooji *et al.* (1984) and McDonald (1981).

The methods used in this paper can also be adapted to accommodate the Weibull distribution; maximum likelihood estimators are available from Law & Kelton (1982). However, the combination of outflow- and fermentation retention times described in Appendix 1, will have to be done by numerical integration. Values similar to those obtained with the gamma retention time distribution are expected, since only two parameters are fitted. The greater effort involved when fitting and using the more complex Weibull function is therefore, unlikely to be justified by a possible better fit.

When iterative least squares techniques are used to fit a model with, for instance more than two parameters, as was done by McDonald (1981), each parameter is fitted in such a way that the best fit of the model is obtained. If realistic estimates in functional terms are obtained for all parameters, it shows that the model used is appropriate. When some of the estimates are biased it shows that in order to achieve a good fit, some of the estimates of parameters had to compensate for others which do not describe all aspects of the model well.

An interesting aspect was observed when parameters of the model of McDonald (1981) was fitted with an iterative least squares method. It showed that the value for b', which estimates the insoluble fermentable fraction, tended to overestimate the *in vitro* estimates for both lucerne (56,1 vs. 38,5 *in vitro*) and maize-cob leaves (79,4 vs. 59,2 *in vitro*). It might be argued that the 72 h *in vitro* method gives an underestimate of potential digestibility. However, the magnitude of these differences has convinced us that the model, although it is flexible enough to describe the fermentation curve accurately, does not always yield accurate estimates of the functional parameters. This happens since the model can not accommodate a phase of increasing activity and has to apply the available parameters to describe the whole fermentation curve. Therefore the parameters loose some of their functional significance. The results of Dhanoa (1988) agree very well with this conclusion.

The first-order model has a very simple solution for combining different independent processes working on the same pool. It is, however, not suitable for describing flow and fermentation kinetics in the rumen, since it gives a biased fit to *in sacco* OM disappearance as well as marker passage at the ileum. More complex models have sufficient flexibility to describe both outflow and fermentation accurately but some have no explicit solution for combining the independent disappearance by both outflow and fermentation from the same pool of fermentable OM. The gamma function has sufficient flexibility to describe both outflow and fermentation accurately. The integer form of the gamma function also has an explicit solution for combining different independent processes working on the same pool.

A correction for the immediately soluble fraction has to be made when the mean retention time of fermentable OM is calculated. When MRT is calculated for both fermentable and non-fermentable OM and rumen fill in terms of OM is known, OM intake may be calculated.

Acknowledgements

The authors are grateful to Mr G.P. Kühn for fitting some of the iterative least squares models. We also thank Profs. W.C. Ellis and J.H. Matis for their friendly co-operation

and for supplying their latest publications on retention time modelling. Dr E.H. Kemm and Mr P.H. Henning are thanked for valuable assistance rendered in the preparation of the manuscript.

Soli Deo Gloria

References

CRONJÉ, P.B., 1983. Protein degradability of several South African feedstuffs by artificial fibre bag technique. *S. Afr. J. Anim. Sci.* 13, 225.

DHANOA, M.S., 1988. Research note on the analysis of dacron bag data for low degradability feeds. *Grass Forage Sci.* 43, 441.

GILL, S.S., CONRAD, H.R. & HIBBS, J.W., 1969. Relative rate of *in vitro* cellulose disappearance as a possible estimator of digestible dry-matter intake. *J. Dairy Sci.* 52, 1687.

GRAHAM, N.Mc.C. & WILLIAMS, A.J., 1962. The effects of pregnancy on the passage of food through the digestive tract of sheep. *Aust. J. agric. Res.* 13, 894.

HOVEL, F.D., NG'AMBI, J.W., BARBER, W.P. & KYLE, D.J., 1986. The voluntary intake of hay by sheep in relation to its degradability in the rumen as measured in nylon bags. *Anim. Prod.* 42, 111.

LAW, A.M. & KELTON, W.D., 1982. Simulation modelling and analysis. McGraw-Hill, New York.

MAHLOOJI, M., ELLIS, W.C., MATIS, J.H. & POND, K.R., 1984. Rumen microbial digestion of fiber as a stochastic process. *Can. J. Anim. Sci.* 64, 114.

MATIS, J.H., 1984. A generalized approach to compartmental modelling based on retention time distributions. In: Modelling ruminant digestion and metabolism. Eds. Baldwin, R.L. & Bywater, A.C. Proc. 2nd Internat. Workshop, University of California, Davis.

McDONALD, I., 1981. A revised model for the estimation of protein degradability in the rumen. *J. Agric. Sci. Camb.* 96, 251.

MEHREZ, A.Z. & ØRSKOV, E.R., 1977. A study of the artificial fibre bag technique for determining the digestibility of feeds in the rumen. *J. Agric. Sci. Camb.* 88, 645.

MERTENS, D.R. & LOFTEN, J.R., 1980. The effect of starch on forage fibre digestion kinetics *in vitro*. *J. Dairy Sci.* 63, 1437.

NRC, 1975. Nutrient requirements of domestic animals. No 5. Nutrient requirements of sheep. National Academy of Sciences, Washington, DC.

ØRSKOV, E.R. & McDONALD, I., 1979. The estimation of protein degradability in the rumen from incubation measurements weighted according to the rate of passage. *J. Agric. Sci. Camb.* 92, 499.

PIENAAR, J.P., ROUX, C.Z., MORGAN, P.J.K., GRATTAROLA, L., 1980. Predicting voluntary intake on medium quality roughages. *S. Afr. J. Anim. Sci.* 10, 215.

PIENAAR, J.P. & ROUX, C.Z., 1984. Inferred mixing compartments in the sheep's digestive tract. *Can. J. Anim. Sci.* 64, 74.

PIENAAR, J.P., ROUX, C.Z. & CRONJÉ, P.B., 1989. Comparison of *in vivo* and *in sacco* methods to estimate mean retention time of fermentable organic matter in the rumen. *S. Afr. J. Anim. Sci.* 19, 71.

POND, K.R., MATIS, J.H. & ELLIS, W.C., 1982. Digesta flow through the ruminant's digestive tract. *Fed. Proc.* 41, 3, Abstr. no 432.

ROUX, C.Z. & MEISSNER, H.H., 1984. Growth and feed intake patterns. I. The derived theory. In: Herbivore nutrition in the tropics and sub-tropics. Eds. Gilchrist, F.M.C. & Mackie, R.I. The Science Press. pp. 672 – 690.

ROUX, C.Z. & PIENAAR, J.P., 1984. Using the gamma function to model both passage rate and fermentation rate for intake prediction. In: Techniques in particle size analysis of feed and digesta in ruminants. p. 176. Ed. Kennedy, P.M. Proc. Workshop, Banff Centre, Banff, Canada.

Appendix 1

Derivation of a general equation describing mean retention time for a single pool on which two gamma processes act simultaneously

For the general approach to retention time modelling, Matis (1984) can be consulted.

Let $f_0(t)$ and $f_1(t)$ be two density functions of retention times acting independently on the same pool. It can then be shown that the combined density function is given by

$$g(t) = f_0(t) + f_1(t) - F_0(t)f_1(t) - f_0(t)F_1(t) \quad \ldots\ldots (12)$$

where $F_0(t)$ and $F_1(t)$ are distribution functions associated with the densities $f_0(t)$ and $f_1(t)$.

Let

$$f_0(t) = [\Gamma(\alpha_0)\,\beta_0^{\alpha_0}]^{-1} t^{\alpha_0 - 1} e^{-t/\beta_0} \quad \ldots\ldots (13)$$

and

$$f_1(t) = [\Gamma(\alpha_1)\,\beta_1^{\alpha_1}]^{-1} t^{\alpha_1 - 1} e^{-t/\beta_1}, \quad \ldots\ldots (14)$$

then, for integer gammas, the mean retention time

$$E(t) = [(\alpha_0 - 1)!\beta_0^{\alpha_0}]^{-1} \sum_{x=0}^{\alpha_1 - 1} 1/x!\,(1/\beta_1)^x (x+\alpha_0)!\,(1/\beta_0 + 1/\beta_1)^{-(x+\alpha_0+1)} +$$

$$[(\alpha_1 - 1)!\,\beta_1^{\alpha_1}]^{-1} \sum_{y=0}^{\alpha_0 - 1} 1/y!\,(1/\beta_0)^y (y+\alpha_1)!\,(1/\beta_0 + 1/\beta_1)^{-(y+1+\alpha_1)} \quad \ldots\ldots (15)$$

where it is assumed that $0! = 1$.

Appendix 2

Application of the gamma retention time model to obtain intake and protein degradation

The method described by Roux & Meissner (1984) to obtain intake from its components *viz.* rumen fill, fermentation and outflow, is based on the calculation of mean retention time for fermentation and outflow.

$$df/dt = Z / \sum_{i=1}^{n} p_i \bar{t}_i \quad \ldots\ldots (16)$$

where df/dt = rate of feed intake
Z = total amount of OM in the rumen
p_i = the proportion of component i in the feed
$\bar{t}_i$ = the MRT of component i
n = total number of components.

The mean retention time for the gamma distribution is $\bar{t}_1 = \alpha_i \beta_i$

where $\bar{t}_i$ = the i th MRT
α_i = the i th shape parameter
β_i = the i th scale parameter of the gamma distribution.

In the case of fermentable OM where both outflow and fermentation act on the same pool and assuming integer gammas with $\alpha_0 = 1$ and $\alpha_1 = 2$, the MRT is given as

$$\bar{t}_1 = (1/\beta_0 + 1/\beta_1)^{-1} + (1/\beta_1)\,(1/\beta_0 + 1/\beta_2)^{-2} \quad \ldots\ldots (17)$$

$$\bar{t}_2 = \alpha_2 \beta_2. \quad \ldots\ldots (18)$$

The following equation then describes intake:

$$\text{Rate of feed intake } df/dt = Z/[p_1 \bar{t}_1 + p_2 \bar{t}_2] \quad \ldots\ldots (19)$$

where

Z = total amount of OM in the reticulo rumen (g)
p_1 = proportion of insoluble fermentable OM in the feed
p_2 = proportion of unfermentable OM in the feed
p_3 = proportion of readily soluble OM in the feed
α_0 = shape parameter for outflow of fermentable OM
α_1 = shape parameter for fermentation of fermentable OM
α_2 = shape parameter for outflow of non-fermentable OM
β_0 = scale parameter for outflow of fermentable OM (h)
β_1 = scale parameter for fermentation of fermentable OM (h)
β_2 = scale parameter for outflow of non-fermentable OM (h)
$p_1 + p_2 + p_3 = 1$ and intake is expressed in g h^{-1}.

The effective degradability of protein, sometimes termed 'p' (McDonald, 1981), can also be obtained from Roux & Meissner (1984) when the gamma function is used. The symbols denote the same as above but in this case the OM of protein is used instead of feed OM.

$$\text{Effective degradability} = p_3 + p_1\,[1/(2\beta_1)]\,\bar{t}_1, \quad \ldots\ldots (20)$$

for $\alpha_0 = 1$ and $\alpha_1 = 2$.

For general integer values

$$\text{effective degradability} = p_3 + p_1\,[1/(\alpha_1\,\beta_1)]\,E(t), \quad \ldots\ldots (21)$$

where E (t) can be obtained from Appendix 1.

This equation replaces the one published by Roux & Pienaar (1984) which is wrong.