

A RUMEN MODEL

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SUMMARY

A rumen model is described, by which parameters as rate constant of degradation, rate constant of passage and intake can be integrated to evaluate the qualitative and quantitative values of these rate constants or to identify knowledge gaps with regard to aspects of processes of rumen degradation, rumen turnover and microbial protein and volatile fatty acid production. Applying the rumen model to data of rumen evacuation studies shows that estimates of rate of degradation derived from nylon bag studies and of rate of passage derived from marker studies were not quantitatively describing feed intake and rumen degradation. It is further described, how by use of a model approach, end products of rumen fermentation as microbial protein, volatile fatty acids and undegraded feed protein can be estimated.

INTRODUCTION

Qualitative knowledge of the ruminants digestive functions has greatly progressed over the last 30 years owing to the combined efforts of microbiologists, nutritionists, physiologists and biochemists. The process of microbial digestion resulting in production of volatile fatty acids and microbial protein has been described by various workers (Hungate, 1966; Van Soest, 1982; Czerkawski and Cheng, 1988; Preston and Leng, 1988). The rumen contains a complex mixture of food materials and micro-organisms, which includes bacteria, protozoa and fungi, many of which interact together in the process of fermenting proteins, soluble carbohydrates and cell walls. Kinetics of processes in the rumen, like rate of passage of liquid and solid phase and rate of degradation, are also studied extensively (Ørskov and MacDonald, 1979; Warner, 1981; Aitchison et al., 1986a, b, c; Tamminga et al., 1989). The kinetic parameters can be integrated into a model to describe intake and ruminal digestion.

A RUMEN MODEL

The capacity of the ruminant animal to ingest, digest and absorb nutrients is controlled by various factors as physiological control factors, physical limitations of and inhibitory factors in the feed. The degradation and passage of feed components and the formation of fermentation end-products in the rumen is of

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major importance in the process of feed utilization. Model descriptions of rumen turnover processes are often based on division of the rumen DM into components with differing passage and degradation characteristics. An example of such a division is given in Table 1.

Table 1 Components of rumen DM.

Component	Composition
Soluble (S)	sugars, protein
Insoluble rapidly degradable (IR)	starch, "storage" protein
Insoluble slowly degradable (IS)	cellwalls, protein associated with cellwalls
Insoluble undegradable (IU)	cellwalls, protein associated with cellwalls

All components have their own rate of degradation (R_d). S has a very high k_d , while IU has a k_d of zero. Fractions IR, IS and IU could be further subdivided into a large and small particle fraction. For cattle particles which are retained on a 1.25 mm sieve are considered to be unable to leave the rumen (Kennedy and Poppi, 1984) and have a rate of passage (k_p) of zero. The rate of passage of the S fraction will be closely related to the rate of passage of the fluid phase.

Degradation of protein and carbohydrates in the rumen will result in production of microbial protein and volatile fatty acids (VFA), while part of the feed protein will leave the rumen undegraded and could be digested and absorbed postruminally. Some examples of modeling of rumen processes will be described in the present paper to demonstrate the various objectives modeling can have:

- evaluation of quantitative and qualitative value of experimentally determined parameters,
- nutritional evaluation,
- prediction of nutrient availability,
- definition of research priorities.

Evaluation of experimentally determined rate constants of passage and degradation of cellwalls

A steady state situation in the rumen means that the rumen pool is constant and that the amount entering the rumen is equal to the amount leaving the rumen. In a steady state situation the rate of intake (k_i = intake/rumen pool) should thus be equal to the rate of disappearance from the rumen, which is equal to $k_d + k_p$, as described by Doyle (1984). This is only true if k_d and k_p are expressed as fraction of the whole rumen pool. If k_d is estimated from in sacco studies by a first order model k_d is the fractional rate of degradation of the potentially degradable fraction and does not refer to the whole rumen pool. A model to estimate k_d from in sacco data is:

$$f_t = f_s + f_d * (1 - e^{-k_d t}),$$

in which f_t is the degraded fraction after t hours of incubation in the rumen and f_s and f_d are the soluble and potentially degradable fraction respectively (Robinson et al., 1986). If such a model is used to estimate the k_d of the cell wall fraction the f_s is zero, since cell walls are by definition insoluble. The k_d of the potential degradable fraction estimated by such a model can be converted to the k_d of the whole rumen cell wall pool by the following formula: fractional rate of degradation of the whole rumen pool (k_d') = $k_d * f_d$.

The k_p is often measured from the excretion characteristics of a marker, that is associated with the particles in the rumen. An often used method is the single dosing of chromium labeled cell walls into the rumen and measurement of the chromium concentration in the faeces at several time intervals after dosing. Preparation of the markers is described by Udén et al. (1980) and the mathematical procedure for estimation of the k_p by Grovum and Williams (1973). The chromium labelled particles are usually of such a size, that they are retained on a sieve of 1 mm. Kennedy and Poppi (1984) proposed, that particles in the rumen of cattle, that are retained on a sieve of 1.25 mm are not leaving the rumen. Hence, the k_p estimated by the usually used marker technique only refers to the particle pool in the rumen, that can potentially leave the rumen and not to the whole rumen cell wall pool. Approximately 30 % of the whole rumen cell wall pool of cattle consuming ammoniated and untreated wheat straw consisted of particles that were retained on a 1.25 mm sieve (Oosting, unpublished). To estimate the k_p of the whole particle pool from the k_p estimated from marker excretion the following formula should be used: rate of passage of the whole rumen particle pool (k_p') = $k_p * \text{fraction of small particles in the rumen particle pool}$.

In Table 2 the actually recorded cell wall intake (NDFI = neutral detergent fiber intake) is compared with the estimate based on the k_p' and the k_d' and the rumen NDF pool for two studies conducted by Aitchisson et al. (1986a, 1986b). The aim of the comparison was to evaluate the value of estimates of rate constants of passage and degradation for explanation of treatment effects. The predicted NDFI is ($k_p' + k_d'$) * rumen NDF pool * 24. The k_p' was calculated from the k_p by assuming that 70% of the rumen particle pool had such a size, that it could potentially leave the rumen.

Table 2 shows, that the qualitative prediction of NDFI by the model was better for the experiment of Aitchisson et al. (1986b) than for the experiment of Aitchisson et al. (1986a). Predicted and observed NDFI are significantly correlated ($r = 0.913$), which indicates, that the model gave reasonable relative predictions. This could, however, mainly be attributed to the high correlation between NDFI and rumen pool size ($r = 0.933$) and not to k_p' and k_d' . The sum of k_p' and k_d' was not significantly correlated to NDFI. The low correlation between the sum of the rate constants

and NDFI could of course be due to the application of a constant fraction of small particles in the rumen particle pool. It can, be concluded from Table 2, that estimates of k_d from *in sacco* experiments and of k_p from marker studies can not simply be used for explanation of treatment effects. Information about rumen pool size and of the average proportion of particles smaller than 1.25 mm in the rumen is required.

The fermentation of feed, especially cell wall constituents, in the rumen is controlled by the fermentation rate and passage rate of digesta (Allen and Mertens, 1988; Aitchisson et al., 1986c). The rumen model could be used to estimate the rumen digestibility of nutrients. The rumen digestibility is equal to $k_d'/(k_d' + k_p')$. Table 3 gives a comparison of actually observed rumen NDF digestibility and model predictions of rumen NDF digestibility by the equation given above.

Table 2 Observed and model predictions of NDF intake.

Feed	Observed NDFI (g/day)	Rumen NDF pool (g)	k_p' (/h)	k_d' (/h)	Predicted NDFI (g/day)
Grass hay ¹					
- early cut	542	423	0.0232	0.0150	388
- late cut	661	650	0.0248	0.0091	529
White clover hay	293	282	0.0209	0.0187	268
Grass hay ²					
- high intake no supplement	551	506	0.0281	0.0145	517
- high intake maize supplement	578	522	0.0279	0.0152	540
- low intake no supplement	367	376	0.0226	0.0131	322
- low intake no supplement	367	399	0.0219	0.0161	364

¹ Aitchisson et al. (1986a); ² Aitchisson et al. (1986b)

Table 3 Observed and model predictions of rumen NDF digestion

Feed	Observed NDFD (g/kg)	k_p' (/h)	k_d' (/h)	Predicted NDFD (g/kg)
Grass hay				
- early cut	748	0.0232	0.0150	393
- late cut	619	0.0248	0.0091	268
White clover hay	797	0.0209	0.0187	472
Grass hay				
- high intake no supplement	626	0.0281	0.0145	340
- high intake maize supplement	601	0.0279	0.0152	353
- low intake no supplement	643	0.0226	0.0131	367
- low intake no supplement	641	0.0219	0.0161	424

Comparison of the observed and predicted rumen NDF digestibility in Table 3 leads to the conclusion, that estimates of k_d' and k_p'

from *in sacco* and marker studies underestimates the rumen digestibility, probably due to overestimation of k_p' and underestimation of k_d' as suggested by Aitchisson et al. (1986c). Overestimation of k_p may be caused by the fact that k_p is estimated by inert markers. Such markers are not subjected to digestion and the production of gases resulting from this digestion. Such gasproduction may reduce the functional specific gravity of feed particles and prevent them from leaving the rumen before a substantial part of the digestion has taken place. Underestimation of k_d may result from the fact that material included in nylon bags is not subjected to particle size reduction due to chewing and rumination (Tamminga, 1993).

Nutritional evaluation: estimation of RDP/UDP value of a protein

Protein in the diet is partly degraded in the rumen and its degradation is affected by factors like solubility, inhibitory substances like tannins etc. and rumen environment. Protein that escapes rumen degradation and that passes to the lower digestive tract plays an important role in high yielding animals, particularly when high biological value protein is fed to cattle. Protein escaping rumen degradation (UDP) can be calculated by using the equation

$$CP_u + (CP_t - CP_s - CP_u) * \frac{k_p}{k_p + k_d}$$

UDP = undegradable protein
 CP_t = total CP
 CP_s = soluble CP
 CP_u = undigestible CP
 k_p = rate of passage of feed protein
 k_d = rate of fermentation of potentially digestible protein.

As with description of NDFI and rumen NDF digestion by the model, the accuracy of prediction of UDP depends very much on the accuracy of prediction of k_d and k_p .

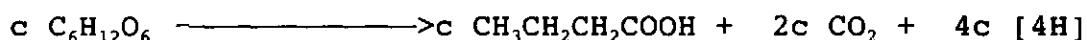
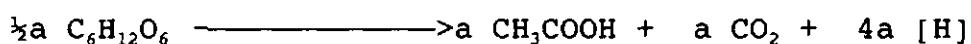
Prediction of nutrient availability: microbial protein synthesis

Microbial protein synthesis is another important function of the rumen, to provide protein to the host animal when digested and absorbed from the lower digestive tract. Now it is established that on average 32 g nitrogen or 200 g microbial protein is synthesized per kg organic matter apparently digested (ARC, 1980), although considerable variation has been reported for individual experiments (Harrison and McAllen, 1980). The efficiency of microbial protein synthesis is however, related to the rate of passage. If passage is relatively slow, the turnover of microbes in the rumen is relatively high due to lysis and

predation by protozoa, which results in a relatively low efficiency of microbial protein synthesis. A quantitative relation between *in vitro* efficiency of microbial protein synthesis and rate of passage is given by Hespell and Bryant (1979).

Prediction of nutrient availability: volatile fatty acids production

The volatile fatty production in the rumen depends on the amount of OM digested. Looking into stoichiometry of hexose fermentation, we find that



(Czerkawski, 1986).

In the above given formulas a, b and c are the molar proportions of acetate, propionate and butyrate of the total volatile fatty acids production.

Thus $(4a + 4c)[\text{H}]$ is produced, $2b[\text{H}]$ is utilized for propionate production and $(4a + 4c - 2b)[\text{H}]$ is left which is converted to methane. Molar proportions play a key role because high fibrous diets result in higher methanogenic VFA. The number of moles of glucose available for digestion in the rumen may be calculated from the whole tract organic matter digestibility (OMD) if it is assumed, that 65% of the whole tract OMD occurs apparently in the rumen (ARC, 1980) and that 1 mole of glucose in carbohydrates has a molecular weight of 162 g:

$$\frac{0.65 * \text{DOM}}{162} = \text{moles of anhydroglucose } (\text{C}_6\text{H}_{10}\text{O}_5)_n$$

(Tamminga and Van Vuuren, 1988).

An example of such a calculation is given below.

Amount of VFA produced

If a cow consumes 8 kg digestible OM, then the apparently rumen digestible OM (ARDOM) is 5 kg, and the ratio of acetate: propionate: butyrate is 70 : 20 : 10, then 5 kg ARDOM with the equivalent to 30.9 moles of $(\text{C}_6\text{H}_{10}\text{O}_5)_n$ and $0.5a + 0.5b + c = 35 + 10 + 10 = 55$ moles of anhydrous glucose are required to produce 100 moles of VFA.

19.7 moles of $(C_6H_{10}O_5)_n = 39.4$ moles of acetate

5.6 moles of $(C_6H_{10}O_5)_n = 11.2$ moles of propionate

5.6 moles of $(C_6H_{10}O_5)_n = 5.6$ moles of butyrate

30.9 moles of $(C_6H_{10}O_5)_n = 56.2$ moles of VFA

Figure 1 Input of feed and output of end products.

Feed Input (5 kg ARDOM)	UDP	-	-	Aminogenic
	Microbial protein	-	1000	Aminogenic
	Moles of acetate	-	39.4	Ketogenic
	Moles of propionate	-	11.2	Glucogenic
	Moles of butyrate	-	5.6	Ketogenic
	Digestible micro lipids	-	-	-
	Digestible feed lipids	-	-	-

Finally, the input and output from the rumen of a cow consuming 5 kg ARDOM in totality has been presented in Figure 1. The feed coming into the rumen consists of CP, carbohydrate, lipids, minerals and vitamins. CP in the rumen is partly degraded to ammonia which is utilized for microbial protein synthesis and partly escapes from the rumen as UDP. Both UDP and microbial protein are aminogenic. Carbohydrates are fermented to VFA, while acetic acid and butyric acids are ketogenic and propionic acid is glucogenic. In addition to microbial protein and VFA some amount of digestible microbial lipids are synthesized.

CONCLUSIONS

A simple rumen model as described here is a tool for integration of feed evaluation parameters. Rumen digestibility, microbial protein synthesis and volatile fatty acid production can be calculated from *in sacco* data in combination with the rate of passage or from the whole tract digestibility. Another aim of a rumen model is to evaluate the value of parameters estimated by various methods. As described in this paper the rate of passage estimated by a marker technique is probably an overestimation and the rate of degradation estimated *in sacco* is probably an underestimation. Many qualitative and quantitative relationships in the rumen are unknown. Modeling could give directions for research, by defining the most important gaps of knowledge.

REFERENCES

- Allen, M.S., and Mertens, D.R., 1988. Evaluating Constraints on Fibre Digestion by Rumen Microbes. *J. Nutr.* 118: 261.
- ARC, 1980. The Nutrient Requirement of Ruminant Livestock. Commonwealth Agricultural Bureaux, Slough, U.K.
- Aitchisson, E.M., Gill, M., Dhanoa, M.S., and Osbourn, D.F., 1986a. The effect of digestibility and forage species on the removal of digesta from the rumen and the voluntary intake of hay by sheep. *British J. of Nutrition* 56: 463-476.
- Aitchisson, E.M., Gill, M., and Osbourn, D.F., 1986b. The effect of supplementation with maize starch and level of intake of perennial ryegrass (*Lolium perenne* cv. Endura) hay on the removal of digesta from the rumen of sheep. *British J. of Nutrition* 56: 477-486.
- Aitchisson, E., Gill, M., France, J., and Dhanoa, M.S., 1986c. Comparison of methods to describe the kinetics of digestion and passage of fibre in sheep. *J. Sci. Food Agric.* 31: 1065.
- Czerkawski, J.W., 1986. An introduction to rumen studies. Pergamon Press, Oxford, U.K., 236 pp.
- Czerkawski, J.W., and Cheng, K.J., 1988. Compartmentation in the rumen, pp. 380. In: P.N. Hakson (ed.): Rumen microbial ecosystem. Elsevier applied science, New York, U.S.A.
- Doyle, P.T., 1984. Some effects of chemical treatment or supplementation on the kinetics of fibre digestion in the rumen, pp. 28. In: The utilization of fibrous agricultural residues as animal feed. Proceedings School of Agriculture and Forestry, University of Melbourne, Parkville, Victoria.
- Grovum, W.L., and Williams, V.J., 1973. Rate of passage of digesta in sheep. 4. Passage of marker through the elementary tract and the biological relevance of rate constants from the changes in concentration of marker in faeces. *British J. of Nutrition* 30: 313-329.
- Harrison, O.G., and McAllen, A.B., 1980. Factors affecting microbial growth yields in the reticulo-rumen, pp. 205-226. In: Y. Ruckebush and P. Thivend (eds): Digestive physiology and metabolism in ruminants. Proceedings 5th International Symposium on ruminant physiology, 3-7 September 1979, Clermont-Ferrand. Lancaster.
- Hespell, R.B., and Bryant, M.P., 1979. Efficiency of rumen microbial growth: influence of some theoretical and experimental factors on Y_{ATP} . *J. of Anim. Sci.* 49: 1640-1659.
- Hungate, R.E., 1966. The rumen and its microbes, Academic Press, N.Y.
- Kennedy, P.M., and Poppi, D.P., 1984. Critical particle size in sheep and cattle. In: P.M. Kennedy (ed.): Techniques in particle size analysis of feed and digesta in ruminants. Canadian Society of Animal Science, occasional publication 1. Edmonton.
- Ørskov, E.R., and McDonald, I., 1979. The estimation of protein degradability from incubation measurement weighted according to passage rate. *J. Agric. Sci. Camb.* 92: 499.
- Preston, T.R., and Leng, R.A., 1988. Matching live stock production system to available resources. ILCA, Addis Ababa, Ethiopia.
- Robinson, P.H., Fadel, J.G., and Tamminga, S., 1986. Evaluation of mathematical models to describe neutral detergent residue in terms of its susceptibility to degradation in the rumen. *Anim. Feed Sci. Techn.* 15: 249-271.
- Udén, P., Collucci, P.E., and Van Soest, P.J., 1980. Investigation of chromium, cerium and cobalt as markers in digesta. *J. of Sci. of Food and Agriculture* 31: 625-632.
- Tamminga, S., and Van Vuuren, A.M., 1988. Formation and Utilization of End Products of Lignocellulose Degradation in Ruminants. *Anim. Feed Sci. and Techn.* 21: 141-159.
- Tamminga, S., Robinson, P.H., Vogt, M., and Boer, M., 1989. Rumen ingesta kinetics of cell wall components in dairy cows. *Anim. Feed Sci. and Techn.* 25: 89.
- Tamminga, S., 1993. Influence of feeding management of ruminant fiber digestibility. Proceedings International Symposium on Forage Cell wall Structure and Digestibility held in October 1991 at Madison, U.S.A.
- Van Soest, P.J., 1982. Nutritional ecology of the ruminant. O and E books, Corvallis Oregon, U.S.A.
- Warner, A.C.I., 1981. Rate of passage of digesta through the gut of mammals and birds. *Nutrition abstracts and reviews*, series B 51: 389.