A RUMEN MODEL

G.P. Singh¹, S.J. Oosting² and S. Tamminga³

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

¹ NDRI-DCND, Kamal-132001, Haryana, India
² Department of Tropical Animal Production, Agricultural University Wageningen, PO Box 338, the Netherlands
³ Department of Animal Nutrition, Agricultural University Wageningen, Haagsteeg 4, the Netherlands
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.

<table>
<thead>
<tr>
<th>Component</th>
<th>Composition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soluble (S)</td>
<td>sugars, protein</td>
</tr>
<tr>
<td>Insoluble rapidly degradable (IR)</td>
<td>starch, &quot;storage&quot; protein</td>
</tr>
<tr>
<td>Insoluble slowly degradable (IS)</td>
<td>cellwalls, protein associated with cellwalls</td>
</tr>
<tr>
<td>Insoluble undegradable (IU)</td>
<td>cellwalls, protein associated with cellwalls</td>
</tr>
</tbody>
</table>

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 ($k_i = \text{intake/rumen pool}$) 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:
A rumen model

\[ f_t = f_s + f_d \times (1-e^{-kt}) \]

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 \((k_d') = k_d \times f_d\).

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 \((k_p') = k_p \times \text{fraction of small particles in the rumen particle pool.}\)

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 \((k_p' + k_d') \times \text{rumen NDF pool} \times 24\) . 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; Aitchison 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.

<table>
<thead>
<tr>
<th>Feed</th>
<th>Observed NDFI (g/day)</th>
<th>Rumen NDF pool (g)</th>
<th>$k_d'$ (/h)</th>
<th>$k_p'$ (/h)</th>
<th>Predicted NDFI (g/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass hay</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- early cut</td>
<td>542</td>
<td>423</td>
<td>0.0232</td>
<td>0.0150</td>
<td>388</td>
</tr>
<tr>
<td>- late cut</td>
<td>661</td>
<td>650</td>
<td>0.0248</td>
<td>0.0091</td>
<td>529</td>
</tr>
<tr>
<td>White clover hay</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- high intake no supplement</td>
<td>551</td>
<td>506</td>
<td>0.0281</td>
<td>0.0145</td>
<td>517</td>
</tr>
<tr>
<td>- high intake maize supplement</td>
<td>578</td>
<td>522</td>
<td>0.0279</td>
<td>0.0152</td>
<td>540</td>
</tr>
<tr>
<td>- low intake no supplement</td>
<td>367</td>
<td>376</td>
<td>0.0226</td>
<td>0.0131</td>
<td>322</td>
</tr>
<tr>
<td>Grass hay</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- high intake no supplement</td>
<td>367</td>
<td>399</td>
<td>0.0219</td>
<td>0.0161</td>
<td>364</td>
</tr>
</tbody>
</table>

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

### Table 3 Observed and model predictions of rumen NDF digestion

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

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

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 Aitchison 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 gas production 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

\[
 UDP = CP_u + (CP_t - CP_s - CP_u) * \frac{k_p}{k_p + k_d}
\]

- \( UDP \) = 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
predatation 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

\[
\begin{align*}
\frac{1}{2}a \text{C}_6\text{H}_{12}\text{O}_6 & \longrightarrow a \text{CH}_3\text{COOH} + a \text{CO}_2 + 4a [\text{H}] \\
\frac{1}{2}b \text{C}_6\text{H}_{12}\text{O}_6 & \longrightarrow b \text{CH}_3\text{CH}_2\text{COOH} + b \text{H}_2\text{O} - 2b [\text{H}] \\
c \text{C}_6\text{H}_{12}\text{O}_6 & \longrightarrow c \text{CH}_3\text{CH}_2\text{CH}_2\text{COOH} + 2c \text{CO}_2 + 4c [4\text{H}]
\end{align*}
\]

(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:

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

(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 \((C_6\text{H}_{10}\text{O}_5)_n\) and \(0.5a + 0.5b + c = 35 + 10 + 10 = 55\) moles of anhydrous glucose are required to produce 100 moles of VFA.
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


